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VERTICAL ZONATION IN WOODLAND BIRD COMMUNITIES

BY M. K. COLQUHOUN AND AVERIL MORLEY

(With 2 Figures in the Text)

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1. INTRODUCTION

In a recent paper (2) it was shown that of the species so far studied in the woodland bird community each occupies a definite vertical niche in the vegetation, and this niche only partially overlaps that of its neighbour in the community. Data collected in Savernake Forest confirmed this finding (3).

The bird community of any British wood is of course quite different in the breeding and non-breeding seasons. As the breeding season approaches there is an influx of 'summer' migrants and exodus of winter visitors, while the males of each member of the community adopt a conspicuous behaviour, which almost invariably involves rising higher in the vegetation than their normal feeding niche. The increased height adds to their conspicuousness, both auditory and visual. Such pronounced conspicuousness, manifested most strikingly by bird song, is often not adopted suddenly, but is gradually built up over a period of weeks. This factor undoubtedly increases the difficulty of analysing the community. As the problem is in any case an extremely intricate one, it seemed best to simplify conditions as much as possible by taking a non-breeding period community as a subject of study. The composition of this community is less complex, i.e. there are fewer species, although there may be more individuals. Moreover, during the short days of autumn and winter the behaviour of the smaller woodland birds is mainly confined to feeding, and we may begin with the hypothesis that each species is occupying its true feeding niche.

2. RELATIVE NICHES: THE ZONAL INDEX

The present study was carried out in Bagley Wood (Berkshire), near Oxford. An area of about 30 acres was selected, consisting of pure *Quercus robur*, with very sparse *Crataegus* secondary, and *Pteridium* and *Rubus*. Sample counts were undertaken throughout the winter of 1941–2, using the same method as before (1, 2), with the difference that all birds seen during the sample counts were recorded in five zones instead of the three strata, tree, shrub, or ground. The zones used were as follows:

Zone 1. Upper canopy: above 35 ft.
Zone 2. Tree: 15–35 ft.
Zone 3. Shrub: 4–15 ft.
Zone 4. Herb: 3 in. to 4 ft.
Zone 5. Ground.

These heights above the woodland floor were of course only approximate, being estimated in the field. It should be noted that in the oak the division between zone 1 and zone 2 is partly a natural one, due to the pyramidal formation of the upper part of the mature tree. The zones are named after the main plant type; these vary in height, so that the upper part of a shrub may sometimes occur in zone 2, and so on. In zone 4 it was interesting to note the slow sinking of the withered *Pteridium* as the winter advanced, with a consequent vertical reduction in cover which must be of considerable importance to ground species.

During the counts each bird was recorded in the zone in which it was first seen, additional notes being kept on its behaviour and subsequent movement. A sample count lasted 1 hr., the observer's walking speed being about 1 m.p.h.; they were undertaken in the mornings, between 9 a.m. and 1 p.m., days of abnormal wind or rain being avoided.

Table 1 gives all the species which totalled over 0·5 individual seen per hour during the period. The recorded abundance is subject to two influences: movement to or from the wood, and variations in specific conspicuousness. Neither factor is important in the present analysis of the community.

Table 1. *Sample counts in Bagley Wood, winter 1941–2. Number of individuals observed per hour*

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
No. of hours ...	3	13	9	6	8	7	4	50
Wood pigeon	0·3	9·2	4·4	—	0·1	0·4	1·0	3·4
Nuthatch	0·3	0·5	0·4	0·2	0·6	1·4	1·2	0·7
Blue tit	4·7	6·3	5·6	3·1	4·8	7·3	10·0	6·0
Long-tailed tit	2·7	2·5	5·1	4·8	4·2	9·0	5·8	4·7
Treecreeper	1·7	1·2	0·9	1·0	1·1	2·6	3·7	1·5
Coal tit	2·3	2·0	2·1	1·8	3·3	3·0	3·8	2·5
Marsh tit	3·0	3·5	3·0	3·0	4·1	4·3	6·0	3·7
Great tit	4·3	3·5	4·9	2·3	4·0	5·5	4·0	4·1
Goldcrest	0·7	0·4	1·2	0·2	0·3	1·0	0·2	0·6
Blackbird	—	1·4	1·1	1·3	1·4	0·3	1·0	1·1
Robin	—	1·4	1·3	1·2	0·1	0·3	0·5	0·8
Wren	2·3	2·4	1·8	1·0	0·8	1·7	2·5	1·8
Other species	(Listed in Appendix)							3·1

Table 2 (*a*) shows the zonal distribution of the species, expressing for each the percentage observed in the various zones. From these figures a series of 'zonal indices' has been calculated in order to show the relative vertical niches of each species. The method of calculating the zonal index depends on an arbitrary choice of vertical units to represent the five zones. If zone 1 (upper canopy) is represented by 100, and zone 5 (ground) by 1, then zones 2, 3 and 4 may be conveniently expressed by 60, 30 and 5 respectively, and the series of numbers will thus be roughly proportional to the median height of the zones they represent. For example, the zonal index of the blue tit is obtained from the calculation

$$\frac{(25\times 100)+(44\times 60)+(26\times 30)+(4\times 5)+(1\times 1)}{100}=59\cdot 4.$$

Table 2. (*a*) *Zonal distribution, Bagley Wood, winter 1941–2. Percentage observed in each zone.* (*b*) *Zonal indices, showing relative vertical niche for each species* (*see text*)

	(*a*) Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	(*b*) Zonal index
Wood pigeon	98	1	1	—	—	99
Nuthatch	49	49	2	—	—	79
Blue tit	25	44	26	4	1	59
Long-tailed tit	26	39	29	4	2	58
Treecreeper	21	50	18	11	—	57
Coal tit	18	43	31	8	—	55
Marsh tit	4	30	42	22	2	36
Great tit	6	18	48	25	3	32
Goldcrest	4	17	55	24	—	32
Blackbird	2	6	23	26	43	14
Robin	—	—	36	40	24	13
Wren	—	—	11	78	11	7

In extreme cases, if all the birds of a species were observed on the ground, the zonal index obtained by this means would be 1, while if the individuals of a species were seen only in the upper canopy the index would be 100. Thus the relative niche of any species is revealed by its zonal index. For instance, the indices (Table 2 (*b*)) reveal at once the striking differences between the blue tit and great tit, a difference which has been emphasized in previous studies.

In the earlier work only three observational strata were used. For the purpose of making further comparison between the blue tit and the great tit indices have been calculated in which tree, shrub and ground zones are represented by 75, 30 and 3 units respectively. The first and last of these numbers correspond to the means of the two upper and two lower zones of the Bagley Wood data, which are in this way brought into line with those for Savernake (3) and Straight Copse (2). These zonal indices are as follows:

	Blue tit	Great tit	Difference	
Bagley Wood (Oct.–Feb.)	60	35	25	Non-breeding season
Savernake (Oct.–Feb.)	54	31	23	Non-breeding season
Straight Copse (Mar.–July)	65	41	24	Breeding season
Savernake (Apr.–June)	60	40	20	Breeding season

It is interesting to find the difference in zonation between the blue tit and great tit in different oak woods and seasons, as recorded by two observers, so nearly constant. The fact that there are slight variations between indices in different woods is hardly surprising, seeing that the habitats are not identical; but the increased indices during the breeding period are undoubtedly due to seasonal changes in behaviour.

3. OAK WOOD COMMUNITIES

(*a*) *Discussion on the vertical niche.* Ecologists have long suspected the existence of vertical niche gradation in forest vegetation, but the extreme mobility of mammals and birds has probably tended to delay analysis of this environment. More recently, Dunlavy (5) divided the vegetation of a university campus into four 'phyto-vertical' zones, recording the zone into which a bird flew on disturbance, the

assumption being that a bird naturally seeks safety in its true niche. Safety, he considered, is the element common both to the refuge site and nest site, both indicating the specific ecological niche of the bird. He dismisses a bird's feeding place as an indication of its vertical habitat, on the grounds that it is very variable. But variants can be measured: such a statement is equivalent to saying that separate vertical niches do not exist, and it seems to us quite out of place to quote as examples of variation such extraordinary phenomena as the periodic movements of lemmings. While not denying that a bird may seek safety in its true niche, we found it difficult to obtain reliable data, and it would have been extremely laborious to accumulate sufficient to be of statistical value.

The nesting niche could be measured exactly, but since it is also variable, the position of a large number of nests would have to be measured. The habitat itself also causes variation; for example, hole-nesting species are dependent on the distribution of holes in the wood. In a *Quercus* wood these holes are likely to be high in the vegetation, but where elder (*Sambucus nigra*) is abundant they will predominate nearer ground level.

Another American worker, Van Deventer, studied the 'horizontal level of activity' for four species (11), and found that this was confined mainly to the lower levels, except for the nuthatch, *Sitta carolinensis*

(*b*) *Zonal abundance.* If the distribution percentage in each zone is multiplied by the total recorded abundance per hour for that species, it is possible to obtain a useful picture of relative zonal abundance, as shown in Table 3 (*a*). No allowance has been made for variations in conspicuousness, but the conspicuousness of three *Parus* species for which data are available is roughly the same; the wren, and to a lesser extent, the robin are much more inconspicuous. It will be seen that each zone has a different dominant* species: the wood pigeon dominates the upper canopy, the blue tit the tree zone, the great tit the shrub zone, the wren the herb zone, and the blackbird the ground. There is also a steady decline in the numerical abundance of each successive dominant species from the upper canopy downwards. The dominant position of the great tit in the shrub zone is here fully revealed; on the other hand it will be noted that long-tailed tits are so distributed over upper canopy, tree and shrub, that they do not dominate any one zone.

Based on the figures in the table below, Fig. 1 shows the vertical distribution and relative abundance of each species.

(*c*) *Vertical communities.* It has already been pointed out that there is a decrease in the abundance of the dominant species in each successive zone.

Table 3. (*a*) *Relative zonal abundance, Bagley Wood, winter* 1941–2. *The dominant species in each zone is printed in heavy type.* (*b*) *Feeding percentage, being the proportion of birds observed feeding*

	(*a*)					(*b*) Percentage observed
	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	feeding
Wood pigeon	**333**	3	3	—	—	1
Nuthatch	34	34	1	—	—	27
Blue tit	150	**264**	156	24	6	64
Long-tailed tit	122	183	136	18	9	76
Treecreeper	32	75	27	17	—	57
Coal tit	45	108	78	20	—	79
Marsh tit	15	111	155	81	7	74
Great tit	25	74	**197**	103	12	56
Goldcrest	2	10	33	14	—	86
Blackbird	2	7	25	29	**47**	4
Robin	—	—	29	32	19	21
Wren	—	—	20	**140**	20	10
Other species	93	96	68	28	25	
Total	853	965	928	506	145	

Since, however, the vertical dimensions of the zones are unequal there is not necessarily a decrease in the population from the canopy downwards. Fig. 2 is a 'community diagram' in which the zones are represented roughly in proportion to their actual vertical depth; the abundance figures, which have been plotted each side of the vertical axis, are taken from Table 3 (*a*) and represent, for each zone, the sum of the values for the species predominating in that zone. For example, in zone 1, only one species predominates, namely, the wood pigeon; in zone 2, the blue tit, long-tailed tit, treecreeper and coal tit predominate; in zone 3, the marsh tit, great tit and goldcrest; in zone 4, the robin and wren; and in zone 5, the blackbird only. Grouping the zonal abundances in this way presents a clearer picture of the actual spatial distribution in the wood; it will be

* Throughout this paper the word 'dominant' is used in its ecological (or, more strictly, numerical) sense. Ecological dominance is not necessarily identical with psychological dominance, which in the *Parus*-*Sitta* flock is fixed and subject to little variation (4).

seen from the diagram that the density of birds increases from the canopy to the shrub level, where it is at its maximum, and it then decreases, although

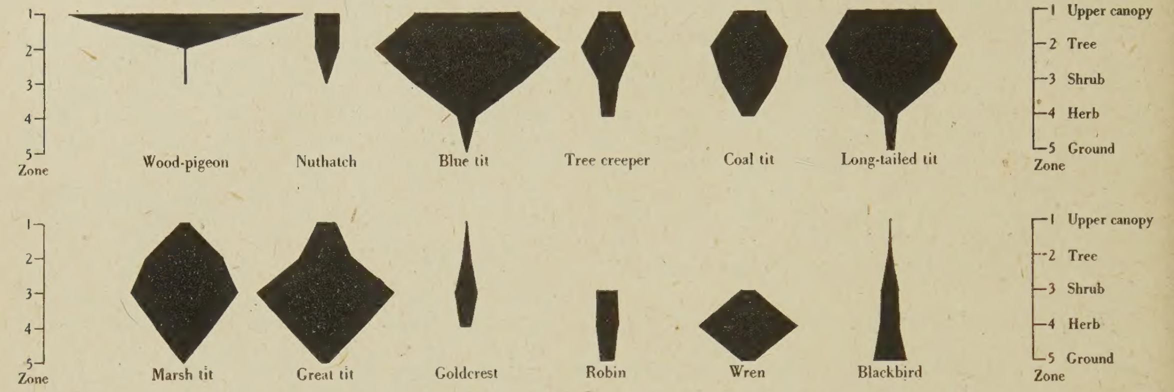

Fig. 1. Zonal distribution and relative abundance, Bagley Wood.

this decrease is less than might be supposed from Table 3. 'Other species' have been excluded because of lack of data, but this omission makes little difference to the shape of the diagram.

If the vertical distribution of the species comprising the Bagley community is considered alone,

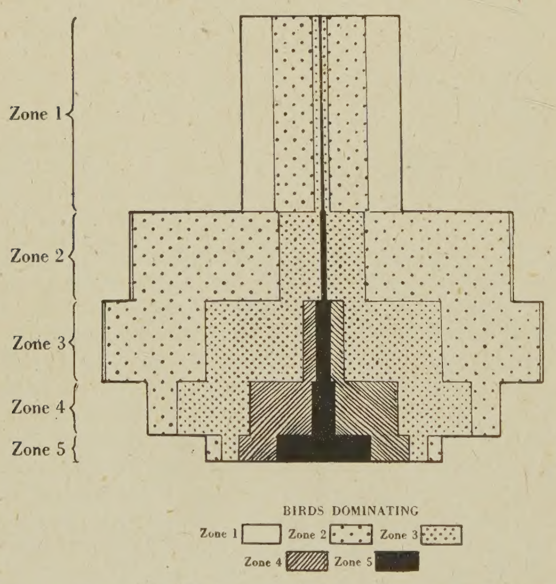

Fig. 2. Community diagram, representing actual vertical abundance of birds in Bagley Wood

ignoring the abundance of these species, an examination of the indices in Table 2 (*b*) shows that the figures tend to fall into groups. Hitherto, both in this paper and in previous studies, the word 'community' has been used as a general term to describe the bird life of a given environment. We now propose that three groups should in fact be regarded as separate communities, a possibility that was envisaged by Elton (6) fifteen years ago. The three communities may be conveniently summarized as follows:

Community	Type genera	Main food zone
Upper canopy	*Columbus-Corvus*	Another habitat
Tree and shrub	*Parus-Sitta*	Tree and shrub
Ground	*Troglodytes-Turdus*	Ground

The upper canopy community consists of ground-feeding species which feed mainly outside the wood; they are therefore often absent from the canopy. The tree and shrub community feeds among foliage, branches and timber of the trees and shrubs. (The number of nuthatches in Bagley Wood was unusually low, but we have retained the term *Parus-Sitta* to describe the normal flock of tits and associated species which forms the bulk of this community.) The ground community finds much of its food on the woodland floor, but may also feed on the herb or shrub.

This is the skeleton of the vertical formation; it will be seen that the basis of the classification of these communities is the food factor. Their zonation may be obscured by the fact that many species are more insectivorous while they are feeding young than at other seasons, and by an abundance of food, such as the larvae crop in early summer. The greatest abundance of *Tortrix* on the oak leaves and the larvae of the shrub zone does in fact coincide with the nesting season.* It is this aspect which suggests the need for non-breeding season studies, when the 'struggle for existence' is probably less intense. The ground community can exist on food from the woodland floor, but it is the first community to feel the effects of a frost, while a prolonged frost or blanket of snow has serious consequences. The

* This statement is based on field observations. A paper now in preparation shows that the maximum number of *Cheimatobia brumata* larvae occurred on hazel (*Corylus*) at the end of May.

upper canopy community, although ground feeding, has a wider foraging range and therefore better chances of adaption (e.g. to agriculture), and thus an improved chance of survival in hard weather. The species comprising this community are capable of strong flight; they may also be equipped with a crop capable of storing food, such as in the pigeons, or be carnivorous in habit, so that they are not obliged to forage without pause. The food supply of the *Parus-Sitta* flock lies mainly on or just below the surface of the branches and twigs, above the extreme frost zone; it is probable that this community suffers least from food scarcity due to cold weather. It is noteworthy that this community is more closely integrated than the other two.

The difference between these three communities is also apparent in Table 3 (*b*), showing the percentage of birds observed feeding.

4. THE TREE AND SHRUB COMMUNITY

(*a*) *The feeding niche.* The assumption that the niche of occurrence in winter is also the feeding niche may best be studied in the tree and shrub community, which is the most important of the woodland communities. For all species except the nuthatch more than half the number of birds recorded had been seen feeding; for some this proportion is more than three-quarters. The percentages are, indeed, higher than had been anticipated, but were probably influenced by the fact that the birds were accustomed to the human observer (**8**), so that disturbance was reduced to a minimum. A comparison between the dominant species of the tree zone and shrub zone will further justify the original assumption. The zonal indices of the blue tit and great tit were found to be 59 and 32 respectively. Table 4 shows that the indices of birds seen feeding only remain unaltered: excepting the nuthatch, the proportion of these two species observed feeding was lower than for all the others of the community. The feeding niche may therefore be taken as identical with the niche of occurrence.

(*b*) *Auditory behaviour.* Although there is no vertical increase in conspicuousness during autumn and early winter, there is a certain amount of auditory behaviour, consisting of calling and 'scolding', which increases with the approach of the breeding season. For the two dominant species, the percentage of birds recorded exhibiting this auditory behaviour was as follows:

	Oct. to Dec. (25 hr.)	Jan. to April (25 hr.)
Blue tit	7	59
Great tit	30	42

There is here a significant difference between the two species which does not appear in the percentages for the whole period (Table 4). At the present time it would be unwise to suggest a reason for the increased auditory behaviour of the great tit in the autumn, since the life history of this species has not yet been intensively studied. In the field the impression was gained that, whereas the blue tit tends to rise, the great tit descends in the vegetation in order to show auditory behaviour; this observation is confirmed by a zonal index based entirely on those birds seen calling and 'scolding', as in Table 4. The blue tit index rises from 59 to 61, but the great tit index falls from 32 to 28.

(*c*) *Composition and structure.* The phenomenon of the temperate woodland bird flock, chiefly composed of species from the four families Paridae, Sittidae, Certhiidae and Regulidae (and probably Picidae), is known in the northern parts of both hemispheres, although the constituents vary geographically. This geographical variation is partly due to a geographical difference in specific gregariousness, species associating with the flock in one part of their range, and apparently abstaining from it, or forming subgroups, in another (**7**, **9**, **10**). While this form of flock is one of the best known and has fallen within the experience of most bird students, little work on its structure has yet been attempted, although it is evident (in the Palaearctic regions) that it is so highly specialized that it closely approaches to a super-organism. For example, the food supply is explored with remarkable efficiency. The woodpeckers, nuthatches and treecreepers, each in their own way, are adapted for feeding on the surface and burrowing fauna of timber and branches. (Although it is difficult to obtain direct proof, we consider that the great spotted woodpecker associates with the *Parus-Sitta* flock: numerically, it is the least abundant, psychologically it is dominant.) Other species obtain their food from the twigs and smaller branches. These species are so closely allied that it is natural to question whether zonation leads to

Table 4. *Comparison between the two dominant species, showing the effect of different behaviour on the zonal index*

				Zonal indices		
	Total no. observed	Percentage singing	Percentage calling and 'scolding'	All birds	Those feeding only	Those calling and 'scolding' only
Blue tit	294	4	23	59	59	61
Great tit	203	5	25	32	32	28

efficiency; but it is likely to be advantageous for one species to search mainly the smaller twigs, another the stouter, lower growth. The blue tit is a smaller bird than the great tit and it may be better adapted for feeding in the upper branches of a wind-swept tree, while the great tit works the less boisterous shrubs; this species also has a stouter bill, better adapted for feeding on fruits and seeds.

Apart from the concept of zonation being advantageous to the *Parus* flock, a view which we put forward rather tentatively at this stage, the explanation of zonation, as with other habits, lies in the past history of the species.

5. CONCLUSION

In our analysis of the woodland flock we have not overstepped a discussion of its composition and structure, because any consideration of its cause would involve the complex subject of social habit, of which there is as yet no real understanding. For instance, it has been said that it is advantageous for forest birds to flock because they thus disturb a maximum of insect life, making it accessible to the members of the flock. It may be said with equal facility that flocking attracts the attention of diurnal predators. The psychological attraction of the flock for the individual bird cannot be denied, and it is unlikely that the advantage of the flock habit is confined to problems of food supply.

In this and the previous studies, based on sample counts, it has been possible to analyse ecological and even behaviour problems by the use of elementary statistics; indeed, it seems to us that the statistical method alone makes analysis possible. If communities are to be analysed further, far more comparative data are needed for different communities and different habitats. It is hoped that students will recognize the need both for standardizing counting methods and for keeping more detailed habitat and behaviour notes on each bird seen. Thousands of birds are being counted annually, but because of the lack of these data the gain in scientific knowledge is slight.

6. SUMMARY

1. From sample counts of birds in Bagley Wood, during which five vertical zones were used, it has been possible to compute a zonal index for each common species. This is the relative niche of occurrence in the vegetation: in the non-breeding season it is identical with the feeding niche.

2. The vertical distribution and relative abundance of each species is shown diagrammatically. Each zone has its own dominant species.

3. Further comparisons are drawn between the blue tit (*Parus coeruleus*) and great tit (*P. major*), which are dominant in the tree and shrub zones respectively. The differences between their zonal indices, in this and in previous studies, was constant for different oak woods and seasons.

4. The bird fauna is analysed, and it is suggested that three separate vertical communities exist in British oak woods. These are the upper canopy community, the tree and shrub community, and the ground community. Food supply is the basis of these communities.

5. The tree and shrub community, containing the *Parus-Sitta* flock, is the most important of the vertical woodland communities.

The paper has been read in draft by Mr P. H. Leslie and Dr Marjory Morris, both of whom have made valuable suggestions.

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APPENDIX

List of species observed in Bagley Wood, mid-October 1941 *to the first week in April* 1942

Carrion crow	*Corvus corone*
Jay	*Garrulus glandarius*
Starling	*Sturnus vulgaris*
Chaffinch	*Fringilla coelebs*
Treecreeper	*Certhia familiaris*
Nuthatch	*Sitta europaea*
Great tit	*Parus major*
Blue tit	*Parus caeruleus*
Coal tit	*Parus ater*
Marsh tit	*Parus palustris*
Willow tit	*Parus atricapillus*
Long-tailed tit	*Aegithalos caudatus*
Goldcrest	*Regulus regulus*
Chiffchaff	*Phylloscopus collybita*
Mistle thrush	*Turdus viscivorus*
Song thrush	*Turdus ericetorum*
Blackbird	*Turdus merula*
Robin	*Erithacus rubecula*
Hedge sparrow	*Prunella modularis*
Wren	*Troglodytes troglodytes*
Green woodpecker	*Picus viridis*
Great spotted woodpecker	*Dryobates major*
Lesser spotted woodpecker	*Dryobates minor*
Tawny owl	*Strix aluco*
Sparrow hawk	*Accipiter nisus*
Wood pigeon	*Columba palumbus*
Pheasant	*Phasianus colchicus*

THE INTERTIDAL ECOLOGY OF BARDSEY ISLAND, NORTH WALES, WITH SPECIAL REFERENCE TO THE RECOLONIZATION OF ROCK SURFACES, AND THE ROCK-POOL ENVIRONMENT

By K. A. PYEFINCH, *University College, Nottingham*

(With 24 Figures in the Text)

CONTENTS

1. INTRODUCTION

An ecological survey was made of the shore of Bardsey Island, North Wales, during the summer months of 1936, 1937 and 1938. Special attention was given to the rate of recolonization of bared rock surfaces and the diurnal variations in the rock-pool environment.

In previous papers on the ecology of Bardsey, some reference has been made to the seashore. A brief account of the main regions of the shore was included in a general account of the island (**21**), and certain aspects of the ecology of the brackish water fauna have been discussed in a later paper (**37**); but beyond these incidental references there are no published accounts of the ecology of this shore, as earlier workers (e.g. Aplin, Coward, etc.) were more particularly concerned with other problems, principally the bird fauna.

The maps in Figs. 1 and 2 show the chief features of the littoral zone and the sites of the investigations. With the exception of small sandy areas within Porth Solfach (on the west coast) and near high-water mark in the Bay of Henllwyn (on the south-east coast), the coast is entirely rocky. According to the account given by Matley (**27**), the shore rocks are almost entirely green slates with grit bands, with small, often isolated intrusions of other types of rock at various points round the coast. On the east coast of the island the rocks slope steeply, but the west coast is in general more gently sloping and in places exposes a considerable width of boulder-covered shore. One coast cannot, however, be considered as definitely more exposed than the other, since parts of the east coast are exposed to the strong tidal currents that run between the island and the adjoining mainland, whereas the west and south coasts are exposed to the full force of westerly and south-westerly gales. Records of wind strength and direction for Holyhead (the nearest point for which such records are available) clearly show the preponderance of high winds from the north-west, west, south-west and south. Local areas, however, both on the west and south-east coasts, are more sheltered, and here opportunity is offered for the development of a more diverse flora and fauna. Such areas are represented by a large part of the shore in the Bay of Henllwyn and a smaller region south of Porth Solfach.

2. GENERAL ECOLOGY OF THE SHORE, AND ITS FAUNA

Practically the whole of the rocky part of the shore is covered, to a varying degree, with the larger brown algae. This reaches its greatest density in the Bay of Henllwyn, where a wide belt of the gently sloping shore is covered, particularly with *Ascophyllum nodosum*. The rocks immediately south of Porth Solfach are also densely covered with algae, but elsewhere the algal covering is less dense, falling to a minimum on the exposed areas of the southern and northern coasts, and on the steeply sloping part of the eastern coast. The dense growth of algae on those parts of the shore which are less exposed has an adverse effect on the fauna. This factor, together with the exposed conditions prevailing elsewhere, is responsible for some paucity in the fauna.

The general zonal sequence of the brown algae (*Pelvetia canaliculata*, *Fucus spiralis*, *F. vesiculosus*, *Ascophyllum nodosum*, *Fucus serratus*, *Laminaria digitata*, *Himanthalia lorea* and *Laminaria saccharina*)

is most clearly seen within the Bay of Henllwyn. The characteristic features of this area are the narrow belt of *Fucus vesiculosus*, lying above the *Ascophyllum*, and the broad belt of *A. nodosum*, which covers most of the littoral zone within the bay. On the west coast, with increasing exposure, this *Ascophyllum* belt becomes narrower and eventually disappears (e.g. near rock 2 and on the north-west coast). Kitching (**22**) has noted the disappearance of *Ascophyllum* under exposed conditions on the coast of Argyll. On those parts of the west coast where the algal covering is at all dense, the coast is too broken to show zonation as diagrammatically as within the Bay of Henllwyn, and no alga can be regarded as dominant over any considerable area of the shore (e.g. immediately north of Porth Solfach there is an admixture of *Fucus serratus* and some *F. vesiculosus* within parts of the *Ascophyllum* zone); and where the exposure is greater some sections of the shore completely lack algal covering (e.g. near rock 2). *Fucus vesiculosus* is variable in its position: as noted above it occurs above *Ascophyllum* in the Bay of Henllwyn (though this zonation does not extend the length of the bay) and within the *Ascophyllum* zone north of Porth Solfach; elsewhere it tends to occur below *Ascophyllum* (e.g. south of Porth Solfach).

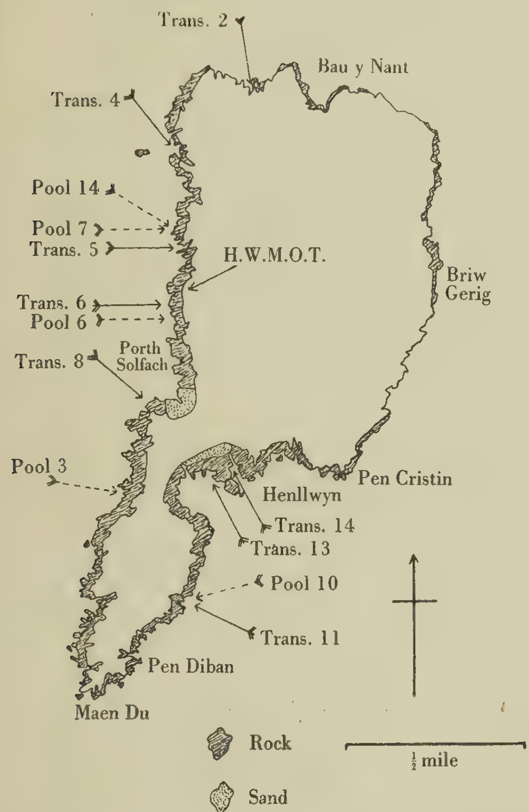


Fig. 1. Sketch map showing the distribution of types of shore, and positions of pools and transects.

The larger brown algae are practically absent on the exposed shores of the southern tip of the island. The rocks in this area are generally inclined at an angle of about 45°, with smooth sloping surfaces towards the north and presenting a series of jagged crevices towards the south. *Lichina pygmaea* occurs, chiefly embedded within the crevices of the rock, though sometimes fully exposed on the surface, patches of *Porphyra umbilicalis* are not uncommon, and isolated plants of *Fucus spiralis* occur here and there (compare the account of rock 6, p. 91 below). Lower down the shore the exposed northerly rock

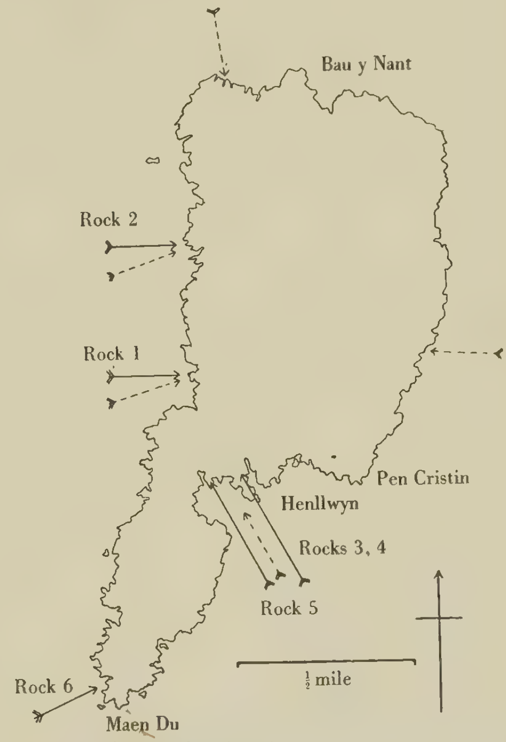


Fig. 2. Sketch map showing the positions of the prepared rock surfaces. The broken arrows indicate the sites where observations of vertical algal zonation were made.

faces are covered with *Lithophyllum*, with associated tufts of *Corallina officinalis*. The two latter algae form the dominant flora of the deep rock pools of this part of the shore.

The outline of the most exposed part of the east coast is very irregular, with numerous small inlets. The flora of larger algae was again much reduced, consisting mainly of scattered patches of *Pelvetia canaliculata* on such boulders as occurred, some *Fucus spiralis* and, near low-water mark, a denser flora of *Laminaria digitata*. The disappearance of *Fucus* on the northerly rock faces was a well-marked feature of algal distribution along this coast.

The sublittoral flora was not examined in any detail, but within Porth Solfach there is always some

accumulation of algae which have been carried into this sheltered bay (**21**), and after a period of south-west gales this increases considerably in amount, and large masses of brown algae are piled high on the beach. *Laminaria digitata*, *L. saccharina*, *Himanthalia lorea* and *Alaria* form the bulk of these masses, but *Fucus serratus* and *F. vesiculosus* were also abundant. There is a fauna of attached or adherent forms associated with this algal mass, which is listed in Table 1 below.

Large numbers of Crustacea commonly associated with such algae (e.g. *Idotea* sp., *Naesa bidentata*, etc.) were also present. This periodic deposition of large quantities of algae produces extreme conditions on this small area of sandy shore, and would seem to be one of the main factors determining the lack of macroscopic fauna.

The fauna of the rocky shore was investigated by means of a series of belt transects, 1 m. in width, of various parts of the coast (Fig. 1), supplemented by more general collections over the adjoining areas. The belt transects were made rather as a means of investigating sections of the shore in detail, than as a means of studying zonation and distribution accurately. It is believed that, using these two methods, a fairly comprehensive idea of the shore fauna has been gained so that the list given in Table 2 may be considered to be reasonably complete, except for the Protozoa and the smaller Crustacea, especially Ostracoda and Copepoda.

Table 1. *Fauna associated with drift-line seaweeds in Porth Solfach*

PORIFERA	Leucosolenia botryoides (Ellis & Solander)
	Grantia compressa (Fabricius)
	Hymeniacidon sanguinea (O. F. Müller)
COELENTERATA	Obelia geniculata (Linné)
	Diphasia attenuata (Hincks)
	Dynamena (Sertularia) pumila (Linné)
	Aglaophenia pluma (Linné)
	Bunodactis verrucosa (Pennant)
CRUSTACEA	Balanus balanoides (Linné)
	B. perforatus Bruguière
MOLLUSCA	Patina laevis (Pennant)
POLYZOA	Bicellaria ciliata (Linné)
	Bulgula turbinata Alder
	Membranipora lineata (Linné)
	M. membranacea (Linné)
	M. pilosa (Linné)
ECHINODERMATA	Amphipolis squamata (Delle Chiaje)
TUNICATA	Botryllus schlosseri (Pallas)
	Amaroucium proliferum Milne-Edwards
	Polyclinum sp. ? aurantium Milne-Edwards

Table 2. *Distribution of the shore fauna*

(The species of rock pools are listed separately, in Appendix 1)

Species	Transect numbers: 2	4+5	6+8	South coast	11	13+14	East coast
PORIFERA							
Leucosolenia botryoides (Ellis & Solander)	—	—	×	—	—	×	—
L. coriacea (Montagu)	—	—	×	—	—	×	—
Sycon ciliatum (Fabricius)	—	—	×	—	—	×	—
Grantia compressa (Fabricius)	—	—	×	—	—	×	—
Oscarella lobularis (Schmidt)	—	—	—	—	—	×	—
*Geodia sp.	—	—	—	—	—	×	—
Adocia cinerea (Grant)	—	—	×	—	—	×	—
*Haliclona clava (Bowerbank)	—	—	—	—	—	×	—
*Amphilectus fucorum (Johnston)	—	—	—	—	—	×	—
Halichondria panicea (Pallas)	—	—	×	—	—	×	—
Hymeniacidon sanguinea (O. F. Müller)	—	×	×	—	×	×	—
COELENTERATA							
Clava multicornis (Forskal)	—	—	×	—	—	—	—
Obelia geniculata (Linné)	—	—	—	—	—	×	—
Laomedea (Campanularia) flexuosa Hincks	—	—	×	—	—	×	—
Dynamena (Sertularia) pumila (Linné)	—	—	×	—	×	×	—
D. (Sertularia) gracilis (Hassall)	—	—	—	—	—	×	—
Kirchenpaueria (Plumularia) pinnata (Linné)	—	—	×	—	—	—	—
Actinia equina Linné	×	×	×	—	×	×	—
Anemonia sulcata (Pennant)	—	×	×	—	—	—	—
Tealia felina (Linné) var. coriacea (Cuvier)	—	—	×	—	—	×	—
Bunodactis verrucosa (Pennant)	—	—	×	—	—	×	—
*Sagartia troglodytes (Price)	—	—	—	—	—	×	—

* Indicates a previous record (1933), not found on the present survey.
× Indicates presence. — Indicates absence.

Table 2 (*continued*)

Species	2	4+5	6+8	South coast	11	13+14	East coast
	Transect numbers						
Platyhelminthes							
Procerodes ulvae (Oersted)	×	×	—	—	—	—	—
Nemertini							
Lineus sp.	—	—	×	—	—	×	—
Amphiporus sp.	—	—	×	—	×	×	—
Annelida							
Harmothoë impar (Johnston)	—	—	×	—	—	×	—
H. spinifera (Ehlers)	—	—	—	—	—	×	—
Pholoë minuta (Fabricius)	—	—	×	—	—	—	—
Eulalia sp.? nebulosa Montagu	—	—	—	—	—	×	
Kefersteinia cirrata (Keferstein)	—	—	—	—	—	×	—
Trypanosyllis zebra (Grube)	—	—	—	—	—	×	—
Nereis pelagica Linné	—	—	×	—	—	×	—
Perinereis cultrifera (Grube)	—	—	×	—	×	×	—
Scolelepis fuliginosa (Claparède)	—	—	×	—	—	×	—
Polydora flava Claparède	—	—	—	—	—	×	—
Cirratulus cirratus (O. F. Müller)	—	—	×	—	×	×	—
Capitella capitata (Fabricius)	—	—	×	—	—	—	—
Arenicola branchialis Audouin & M.-Edwards	—	—	×	—	—	—	—
Fabricia sabella (Ehrenberg)	—	—	×	—	—	—	—
Pomatoceros triqueter (Linné)	—	—	×	—	—	×	—
Spirorbis borealis Daudin	—	×	×	×	×	×	—
Clitellio arenarius O. F. Müller	—	×	×	—	—	×	—
Peloscolex benedeni Udekem	—	—	—	—	—	×	—
Marionina semifusca (Claparède)	—	×	×	—	—	—	—
Crustacea							
*Chthalamus stellatus (Poli)	—	—	—	—	—	—	×
Balanus balanoides (Linné)	×	×	×	×	×	×	×
Tanais cavolini M.-Edwards	—	—	×	—	—	×	—
Gnathia sp.? maxillaris (Montagu)	—	—	—	—	—	×	—
Naesa bidentata (Adams)	—	—	×	—	—	×	—
Idotea granulosa Rathke	—	×	×	—	—	×	—
I. neglecta G. O. Sars	—	—	×	—	—	—	—
Jaera marina (Fabricius)	×	×	×	—	×	×	—
Ligia oceanica (Linné)	—	×	×	—	×	×	—
Hemioniscus balani (Spence Bate)	—	—	—	×	—	—	—
Stenothoides latipes (Chevreux)	—	—	×	—	—	×	—
Gammarus marinus Leach	×	×	×	—	×	×	×
Orchestia gammarella (Pallas)	—	×	—	—	—	—	—
O. mediterranea A. Costa	—	—	×	—	—	—	—
Hyale nilssoni (Rathke)	—	—	—	—	—	×	—
Amphithoë rubricata (Montagu)	—	—	×	—	—	×	—
Leander serratus (Pennant)	—	—	×	—	—	×	—
Porcellana platycheles (Pennant)	—	—	×	—	—	×	—
P. longicornis (Linné)	—	—	×	—	—	—	—
Eupagurus bernhardus (Linné)	—	—	×	—	—	×	—
Portunus puber (Linné)	—	—	×	—	—	—	—
Carcinus maenas (Pennant)	×	×	×	—	×	×	×
Cancer pagurus Linné	—	—	×	—	×	×	×
Insecta							
Lipura maritima Guerin	—	×	×	—	×	×	—
Aëpophilus bonnairei Sig.	—	—	—	—	—	×	—
Aëpus robini Laboulb	—	—	×	—	—	—	—

* Indicates a previous record (1933), not found on the present survey.
× Indicates presence. — Indicates absence.

Table 2 (*continued*)

Species	Transect numbers 2	4+5	6+8	South coast	11	13+14	East coast
PYCNOGONIDA							
Anaplodactylus virescens (Hodge)	—	—	×	—	—	—	—
NEMATODA							
Enoplus sp.	—	—	—	—	—	×	—
MOLLUSCA							
Lepidochitona cinereus (Linné)	—	—	—	—	—	×	—
Lepidopleurus cancellatus (Sowerby)	—	—	×	—	—	—	—
Acanthochitona crinitus (Pennant)	—	—	×	—	—	—	—
Anomia ephippium Linné	—	—	—	—	—	×	—
Mytilus edulis Linné	—	×	×	—	×	—	—
Musculus discors (Linné)	—	—	×	—	—	×	—
Lasaea rubra (Montagu)	—	—	—	—	×	—	—
Patella vulgata Linné	×	×	×	×	×	×	×
Patina pellucida (Linné)	—	—	×	—	—	×	—
Gibbula cineraria (Linné)	—	×	×	—	×	×	
G. umbilicalis (Da Costa)	—	×	×	—	—	×	—
Littorina neritoides (Montagu)	—	×	—	×	—	—	×
L. saxatilis (Olivi)	×	×	×	×	×	×	×
L. littoralis (Linné)	—	×	×	—	×	×	—
L. littorea (Linné)	×	×	×	—	×	×	—
Cingula semicostata (Montagu)	—	—	×	—	—	×	—
C. cingillus (Montagu)	—	×	×	—	×	×	—
Rissoa sp. ? parva (Da Costa)	—	×	×	—	—	—	—
Turbonilla elegantissima (Montagu)	—	—	—	—	—	×	—
Nucella lapillus (Linné)	—	×	×	—	×	×	×
Phytia myosotis (Draparnaud)	—	—	—	—	×	—	—
Aplysia punctata (Cuvier)	—	×	×	—	-	×	—
Archidoris britannica (Johnston)	—	—	×	—	—	—	—
POLYZOA							
Membranipora lineata (Linné)	—	—	×	—	—	×	—
M. pilosa (Linné)	—	—	—	—	—	×	—
Cellaria fistulosa (Linné)	—	—	×	—	—	—	—
Schizoporella unicornis (Johnston)	—	—	—	—	—	×	—
S. hyalina (Linné)	—	—	×	—	—	—	—
Alcyonidium hirsutum (Fleming)	—	—	—	—	—	×	—
Flustrella hispida (Fabricius)	—	—	—	—	—	×	—
Valkeria uva (Linné)	—	—	—	—	—	×	—
Pedicellina cernua (Pallas)	—	—	—	—	—	×	—
ECHINODERMATA							
Asterina gibbosa (Pennant)	—	—	×	—	—	×	—
Amphipolis squamata (Delle Chiaje)	—	—	×	—	—	×	—
Psammechinus miliaris (Gmelin)	—	—	×	—	—	—	—
TUNICATA							
Botryllus schlosseri (Pallas)	—	—	×	—	—	×	—
Amaroucium proliferum Milne-Edwards	—	—	×	—	—	×	—
Didemnum gelatinosum Milne-Edwards	—	—	×	—	—	×	—
FISH							
Anguilla vulgaris Turton	—	×	—	—	—	—	—
Ammodytes Sp.	—	—	—	—	—	×	—
Blennius pholis Linné	—	—	×	—	—	—	—
Cottus sp.	—	—	—	—	—	×	—

* Indicates a previous record (1933), not found on the present survey.
× Indicates presence. — Indicates absence.

Table 2 clearly shows that only in two areas of the shore, in the Bay of Henllwyn (transects 13 and 14) and an area immediately round Porth Solfach (transects 6 and 8), is there any diversity of fauna. Elsewhere, and particularly on the south and east coasts, the fauna is severely reduced. Even within the Bay of Henllwyn and round Porth Solfach conditions are not ideal, since in the former area the substratum is mainly flat, fixed masses of rock and in the latter there is some degree of exposure: conditions which must exclude many of the more delicate shore forms.

Comparison may be made between the shore fauna of Bardsey and that of other parts of Cardigan Bay, of which the fauna has been investigated by Walton (**44**). Table 3 compares these two areas statistically.

Table 3. *The shore faunas of Bardsey and Cardigan Bay*

	Number of species		
	Cardigan Bay	Bardsey	Species in common
Porifera	5	11	3
Coelenterata	15	11	6
Platyhelminthes	2	1	0
Nemertini	4	2	2
Annelida	14	19	6
Gephyrea	1	0	0
Crustacea	34	26	12
Insecta	0	4	0
Pycnogonida	2	1	0
Nematoda	0	1	0
Mollusca	47	23	13
Polyzoa	9	9	3
Echinodermata	4	3	0
Tunicata	3	4	1
Fish	16	5	3
Total	156	120	49

(The Bardsey list includes forms found living in the rock pools, but excludes those pool forms which clearly had been washed in (see Appendix 1) and the fauna associated with the algal masses in Porth Solfach (see Table 1).)

It is evident, from Walton's account, that the range of environment available for his investigation, including, as it did, areas of sandy beach, was considerably wider than that on Bardsey. The greatest difference between the two areas lies in the Molluscs, but his list included estuarine forms, sand-living Lamellibranchs and several Opisthobranchs, which are represented on the exposed shores of Bardsey only by *Aplysia punctata* and *Archidoris britannica*. Apart from this difference there is an approximate numerical equivalence between the two areas, but the small number of species common to the two areas should be noted.

Several investigators, notably Colman (**5**) and Elmhirst (**8**), have drawn attention to a bimodal type of distribution of shore forms, producing a greater diversity of fauna near high- and low-water marks than at mid-tide level. Investigation of the number of species present at various levels on the shore of Bardsey does not indicate any such distribution in the present case. On the Henllwyn shore there is, in general, a progressive increase in the numbers of species present from high-water mark down to low-water mark, whereas round Porth Solfach the mid-tide levels possess the greatest diversity of fauna, a condition similar to that found by Fraser (**9**) for Ostracods and Copepods. Colman (**6**) has also shown the existence of a high density in animal populations associated with *Ascophyllum*.

Some species appear to be confined to the west and north-west coasts of the island (e.g. *Clava multicornis*, *Anemonia sulcata*, *Procerodes ulvae*, *Marionina semifusca*, *Archidoris britannica* and *Psammechinus miliaris*), and some (e.g. *Jaera marina*) are much commoner on these coasts than on the east. This is partly due to the more favourable nature of parts of the west coast (particularly those parts with a boulder shore) but in some cases (e.g. *Procerodes ulvae*, *Jaera marina* and possibly *Marionina semifusca*) the presence of small fresh-water streams flowing over the shore on this coast (the general direction of land drainage is towards the west (Pyefinch, **37**)) would seem to be an important factor.

Most of the forms listed in Table 2 are common shore forms, but points of interest in the biology or distribution of the following species merit a brief description.

COELENTERATA

Dynamena pumila is associated particularly with *Ascophyllum nodosum* except where the shore was in any way muddy.

Kirchenpaueria pinnata is recorded as the most abundant Plumularian at Plymouth (**26**), but it is not recorded for Cardigan Bay. Its status as a shore fauna on Bardsey is doubtful, its only occurrence being on *Laminaria* holdfasts on the west coast.

PLATYHELMINTHES

Procerodes ulvae occurs particularly on the north, north-west and west coasts of the island. Its occurrence and distribution on the shore north of Porth Solfach have been described previously (**37**), but it also occurs in some abundance both in rock pools (e.g. pool 7, where there is considerable variation in the chloride content, see p. 99 below), and also on the shore of gullies on the north and north-west coasts. In one of these gullies conditions are very similar to those investigated earlier; but in others no fresh water was flowing over the shore at the time of examination, though during wet weather these parts of the shore are probably periodically flooded.

ANNELIDA

Harmothoë spinifera is not typically a shore form, but is recorded as common in dredgings at Plymouth (**26**). On Bardsey it occurred in pool 6 (see p. 96

below) and possibly also within the Bay of Henllwyn near low-water mark.

Spirorbis borealis was noted as especially common on *Fucus serratus*, but less common on other species of *Fucus*. This difference was especially marked on rock 3, where *F. vesiculosus* and *serratus* (see Fig. 7) were growing side by side. It seems possible that the typical habitat of *F. serratus*, on those parts of the shore where water movement is continuous, might explain this association, since such conditions would provide a particularly favourable environment for *Spirorbis*.

Marionina semifusca. Stephenson (**41**) records this Oligochaete as present under moist stones near high-water mark in places where fresh water runs on to the shore. On Bardsey it was generally distributed along the west coast, particularly near Porth Solfach. With one exception, it occurred near high-water mark.

CRUSTACEA

Balanus balanoides occurs all round the coast and is especially common on the most exposed stretches to the east and south (compare Kitching, **22**, and Stephenson, **42**), but is reduced in numbers where there is much algal growth and is absent altogether from those parts of the shore (e.g. the Bay of Henllwyn) where *Ascophyllum* is the dominant alga. Kitching (**22**) has pointed out that *Balanus balanoides* is unable to exist on smooth rock surfaces in the immediate neighbourhood of either *Ascophyllum* or *Fucus serratus*. The rubbing of the fronds of these algae seems to prevent settling of the cypris larvae, but, as the physical conditions on the rock surface set up either by this means, or by the rapid movement of water over an exposed rock surface (where settling of the cypris takes place readily) would not appear dissimilar, the factors governing the settling of these larvae would seem to merit investigation.

Gnathia sp.? *maxillaris* was found in burrows in *Halichondria panicea*, a similar habitat to that given by Walton (**44**).

Jaera marina. Moore (**28**) states that this Isopod is to be found only on rocky or gravelly coasts where fresh water runs in. On Bardsey, though it occurs in small numbers on the east coast, it is most common on the west coast, where it becomes progressively commoner from Porth Solfach northwards. Its distribution is very similar to that of *Procerodes ulvae*, and it occurs in greatest density where there are variations in salinity (e.g. pool 7, gullies of the north and north-west coasts).

Hemioniscus balani. Moore (**29**) only recorded this parasite once on the Isle of Man, though he examined large numbers of barnacles. In the present instance it was found only once, but, as no special search was made, no comment can be made on its abundance.

MOLLUSCA

Patella vulgata. Jones, McCance & Shackleton (**20**) have demonstrated the presence of iron and silica in the radula of the limpet, and have suggested that these constituents are derived from *Enteromorpha*, which contains appreciable quantities of these substances, and which forms part of the food of *Patella* (Orton, **34**). The distribution of adult *Patella* does not seem to be limited by the availability of *Enteromorpha*; large numbers of *Patella* were collected from several points on the shore of Bardsey, some were situated near *Enteromorpha*, for others this alga was not available, but tests made on their radulae for the presence of iron (using $K_3Fe(CN)_6$, $(NH_4)_2S$ and KCNS according to the methods of Jones and others) were uniformly positive. Further, no significant differences could be found in the results obtained from tests made on the radulae of smaller (1·9 cm. diameter) or larger (5·2 cm. diameter) specimens. There can thus be no direct relationship between the food plant available and the chemical composition of the radula.

Gibbula cineraria and *umbilicalis*. Table 2 shows that *G. cineraria* is rather more widely distributed on Bardsey than *G. umbilicalis*, and the detailed records of the transects show that the former species is much more common, as *G. umbilicalis* occurs mainly as isolated specimens. This relationship is generally similar to that given for the Isle of Man (**29**), but is the reverse of that found by Walton (**45**) in Cardigan Bay.

POLYZOA

Cellaria fistulosa is not usually found on the shore: its only occurrence on Bardsey was in a rock pool near low-water mark south of Porth Solfach.

ECHINODERMATA

Amphipolis squamata. This was the only Echinoderm occurring at all commonly on the shore: often it occurred in association with *Corallina* in more sheltered areas.

TUNICATA

Didemnum gelatinosum. Recorded twice, attached to *Laminaria* holdfasts at low-water mark.

This discussion of general shore ecology has been confined entirely to that of the rocky parts of the shore. The sandy areas indicated in Fig. 1 were also examined and certain physical (size of sand grains, rate of evaporation, rate of capillary rise and water content) and chemical (*p*H and salinity of the interstitial water) data measured, but, as these areas both were barren of macroscopic fauna, discussion of these results has been omitted.

3. RECOLONIZATION OF BARED ROCK SURFACES

(*a*) *Description*

In April 1936 a series of rock surfaces, scattered along the western, southern and south-eastern coasts of the island, were completely denuded of their fauna

and flora. Six surfaces were prepared in this way and they were chosen to show as much variation as possible in (*a*) position on the shore, (*b*) angle of slope, (*c*) degree of exposure, and (*d*) extent of fissuring. Table 4 summarizes the main physical features of the surfaces prepared.

Table 4. *Characteristics of rock surfaces*

No.	Position	Surrounding flora	Area bared in.	Angle of slope	Extent of fissuring	Exposure
1	West coast, north of Porth Solfach	*Ascophyllum*	36 × 36	Less than 20°	Some: irregular surface	Moderate
2	West coast, north of rock 1	*Fucus spiralis*	36 × 27	*c.* 20°	Deep fissures	Moderate—considerable
3	Bay of Henllwyn	*Ascophyllum*	36 × 22	Mostly at 45°	Irregular surfaces	Slight
4	Bay of Henllwyn	*Ascophyllum*	48 × 40	Practically flat	A few deep fissures	Slight
5	Henllwyn, south of rocks 3 and 4	*Pelvetia*	45 × 30	Less than 20°	Some	Slight
6	South end of island	*Corallina* and *Lithophyllum*	47 × 40	75–80°	Some deep fissures	Full

Figs. 3–10 illustrate some of the more important stages in the recolonization of these surfaces. Figs. 3–6 trace the sequence of changes for rock 2 from July 1936 to April 1938 and Figs. 7–10 comparable stages for the other rocks.

On rock 2 the regrowth from April to July 1936 was characterized by the appearance of the green algae *Ulva lactuca* and *Cladophora* sp. (probably *rupestris*), the areas covered by these algae being those where moisture was most persistent, either in or near the small pools on the rock surface or in the deeper crevices. *Fucus* was beginning to appear and again was mainly confined to the crevices, though some sporelings had become attached on the more exposed surfaces. At this stage the fauna consisted of small *Balanus balanoides* (derived from the spat-fall which had taken place after the rock had been bared in early April), confined, except towards the lower border of the rock, to the crevices. A few *Patella* and two specimens of the anemone *Actinia equina* completed the attached fauna; errant forms included *Littorina saxatilis* and *L. littoralis* in one of the small pools. If the *Patella* which migrate on to a denuded area at this early stage remain there at all permanently, it is possible that they may affect the course of recolonization, since Knight & Parke (25) have shown that limpets may carry the basal remains and small fragments of the thalli of a large number of plants. This cannot have been of much importance in the present instance.

Nine months later, in April 1937, the whole appearance of the surface had changed owing to the growth and spread of *Fucus spiralis*, which covered much of the upper and lower parts of the rock, though individual plants had become established principally in the deeper crevices. Green algae were absent, but some growth of *Corallina* had appeared in some of the pools. Just over four times the number of *Patella vulgata* were present, groups of *Balanus balanoides* were scattered over the surface and small numbers of *Actinia equina* had become attached. *Littorina saxatilis* and *Nucella lapillus* were also found. Changes between April and July 1937 were, on the whole, slight. The area covered

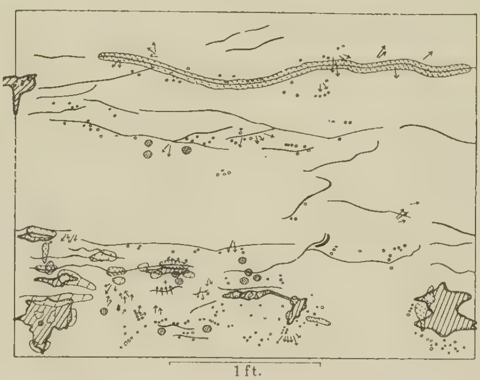
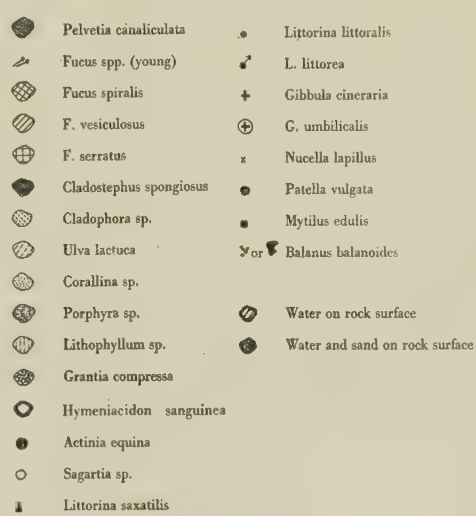


Fig. 3. Rock 2, July 1936. (Each symbol for limpets in Figs. 3–10 shows one individual.)



Key to symbols used in Figs. 3–10

with *Fucus spiralis* had increased, and, though small patches of *Cladophora* and *Enteromorpha compressa* occurred in some of the pools, the green algal growth was appreciably less than in 1936. The numbers of *Patella* and the areas covered with *Balanus balanoides* had increased. *Nucella lapillus* and *Littorina saxatilis*, the latter especially abundant in the *Fucus*-covered areas, were also present.

The condition of the rock surface in April 1938 is shown in Fig. 5, and emphasizes the increase in the area covered with *Fucus spiralis*. The general fauna of the rock remained the same, though small specimens of *Mytilus edulis* and *Sagartia* sp. (? *troglodytes*) had become established in the larger pools. At this stage, with the increased growth of *Fucus*, it was becoming difficult accurately to estimate the numbers of *Patella* or to record the areas covered by *Balanus*. This difficulty had increased in the following July and was one of the reasons why no detailed plan of

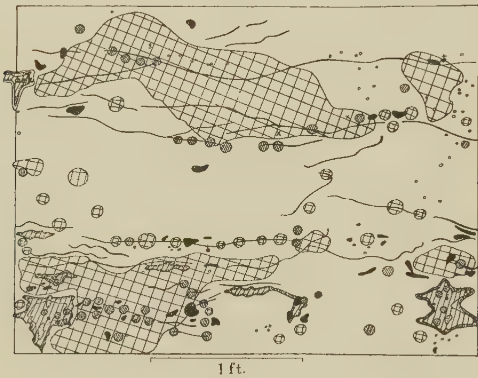


Fig. 4. Rock 2, April 1937.

the whole rock surface was made at that time, the other being the lack of major changes in the period April to July. *Fucus spiralis* had almost entirely covered the surface (much of the increased area covered in these later stages is due to an increase in size of plants established earlier, rather than to an extensive establishment of new plants) and was markedly denser than that of surrounding rocks. This increased density of *F. spiralis* was probably purely a temporary phase, since a closer examination showed that some of the plants were only loosely attached, and thus would be likely to be broken away by the autumn and winter gales, to which this rock would be exposed.

Briefly, the changes occurring on this rock surface in the two years from July 1936 to July 1938 are:

(*a*) An initial growth of green algae, particularly confined to the small pools and the deeper crevices.

(*b*) This was accompanied by the appearance of *F. spiralis* which spread and grew steadily so as finally to cover the whole rock surface. In July 1938 this growth was rather denser than on neighbouring surfaces.

(*c*) Accompanying these changes in the flora was a steady increase in the sessile members of the fauna. The later stages of recolonization favour the appearance of a higher proportion of errant forms.

Some features of this sequence of changes for the whole rock surfaces can be traced, in miniature, in those taking place in the pools on the surface. Fig. 6 shows one such sequence. The initial colonization by *Ulva* and *Cladophora* is well marked (Fig. 6*a*); a

Fig. 5. Rock 2, April 1938.

little *Cladophora* again appeared in July 1937 but no green algae were present in 1938. *Corallina officinalis* first appeared in April 1937 and persisted throughout the time the pool was under observation, showing a more extensive growth in April than in July each year. The floor of the pool was initially almost

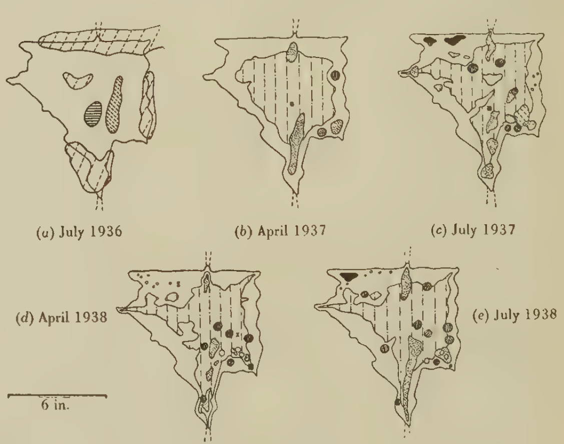


Fig. 6. Rock 2. Sequence of recolonization of rock pool, July 1936 to July 1938.

completely covered with *Lithophyllum*, but the area covered by this alga progressively decreased (cf. Fig. 6 *b*, *e*). The fauna of the pool consisted of *Actinia equina*, *Mytilus edulis* (which were present in April 1937), *Balanus balanoides* (July 1937) and *Sagartia* (April 1938). Both in this pool and in others on the same rock the latter was associated with *Mytilus*, an association noted by Newbigin (**32**).

The general course of recolonization of rocks 1, 3 and 4 was similar to that described in detail for rock 2. Figs. 7 and 8 show the stage reached by rocks 3 and 4 in April 1938—a stage corresponding to the last stage figured for rock 2. On rock 3 recolonization of the bared surface was complete, but was incomplete on one side of rock 4, where the surface was rubbed by the fronds of *Ascophyllum* growing on adjacent rocks. This may be an effect

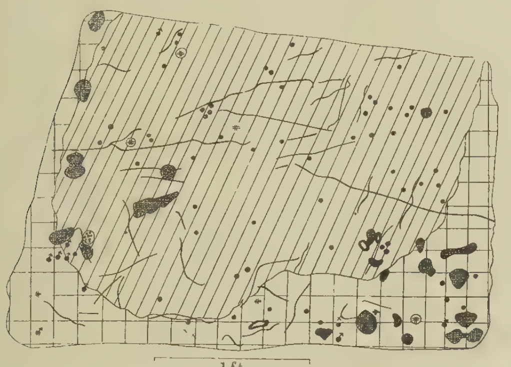


Fig. 7. Rock 3, April 1938.

similar to that noted by Kitching (22) and mentioned earlier (p. 88), though in this instance the overlying *Ascophyllum* fronds would also reduce the light intensity. The most striking feature of the recolonization of these rocks is the nature of the dominant algal growth. Both are situated within the *Ascophyllum* zone, rock 4 nearly 5 m. from its upper edge and rock 3 6·5 m. from its lower edge, but in

Fig. 8. Rock 4, April 1938.

both cases the dominant growth of alga after recolonization was that of *Fucus vesiculosus*. On rock 4 *F. vesiculosus* alone was present, but on rock 3 there was also a fringe of *F. serratus* (Fig. 7) (the relative distribution of *F. vesiculosus* and *serratus* is in accordance with the observation of Rees (39) that the latter species 'is practically confined to regions where there is considerable water movement, apart from the regular ebb and flow'). This point is discussed further below. The rate of growth of *F. vesiculosus* was appreciably higher at rock 3 than elsewhere (Fig. 13), and the rock surface was almost completely (95 %) covered as early as July 1937 (Fig. 12). On both rocks there was a moderately dense errant fauna, *Littorina littoralis* being especially abundant on rock 4.

Rock 5, situated within the *Pelvetia* zone south of rocks 3 and 4 (Fig. 2), presents a marked contrast to the other rocks described. From April 1936 to the following July recolonization was rapid, so that the area of rock covered at that time was rather greater than that of most other rocks, but afterwards the *Pelvetia* spread very slowly (only 13 % of the rock surface being covered by July 1938), and the growth rate of individual plants was equally slow. Fig. 9, which shows the surface of the rock in April 1938, emphasizes both the general confinement of *Pelvetia* to the rock crevices and the absence, apart from a few specimens of *Littorina saxatilis*, of fauna.

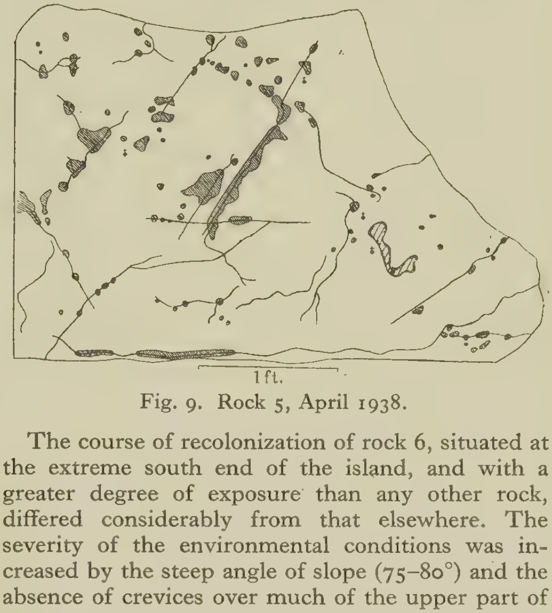


Fig. 9. Rock 5, April 1938.

The course of recolonization of rock 6, situated at the extreme south end of the island, and with a greater degree of exposure than any other rock, differed considerably from that elsewhere. The severity of the environmental conditions was increased by the steep angle of slope (75–80°) and the absence of crevices over much of the upper part of the area studied. Mechanical shock due to wave action was always considerable, and during bad weather it was severe. The water ran rapidly down the steeply sloping surface though, because of the configuration of the surrounding rocks, it took a little time to drain away from the V-shaped lower edge. The earlier stages of recolonization (e.g. July 1936) were characterized by the development of some small *Fucus* (? *spiralis*) plants, particularly near the upper edge, several patches of *Porphyra* roughly half-way down the rock and two small areas of *Corallina* near the base. *Cladophora* was also present in two very small patches, and other specimens of this alga, attached to the shells of *Patella*, were also present. There were a few specimens of *P. vulgata*. Later stages of recolonization (Fig. 10) showed the development of an extensive covering of *Balanus*

balanoides over the upper part of the rock and some increase in the numbers of *Patella*. Counts showed that the *Patella* population reached a maximum in

Fig. 10. Rock 6, April 1938. The area bounded by a continuous line in the upper part of the figure is that covered with *Balanus balanoides*; the broken line indicates the original upper limit of *Corallina*.

April 1938, a condition which is contrasted in Fig. 11 with that found on rock 2 where there was a steady increase in the numbers of *Patella* throughout the period of survey.

Only two specimens of *Fucus spiralis* had survived (and these had disappeared three months later): *Corallina officinalis*, the most prominent member of the flora of the lower half of the rock, was spreading steadily. Rees (**39**) has pointed out that algae such as *Corallina*

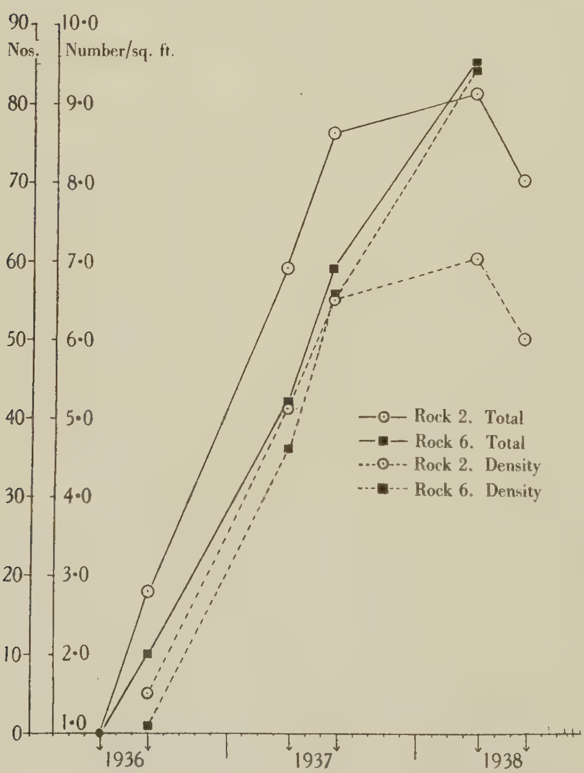


Fig. 11. Rocks 2 and 6. Density of *Patella* populations.

can find lodgement on a steeply sloping rock surface, since they possess a creeping basal portion which can become embedded in some minute crack, whereas a disk-like basal holdfast is less effective (e.g. *Fucus*). In this connexion it is interesting to note that many of the tufts of *Corallina* were associated with *Lithophyllum* or with *Patella* shells, substrata which would offer small crevices.

(*b*) *Discussion*

Several studies have been made recently of the recolonization of denuded or newly created areas within the littoral or sublittoral zones (Wilson (**47**), Pieron & Huang (**35**), Hatton (**16**), Herpin (**17**), Kitching (**23**), Moore (**30**) and Moore & Sproston (**31**)), but not all of these are strictly comparable with the present investigation. Wilson confined his attention to the earliest stages of the process, Herpin, Moore and Moore & Sproston have described the recolonization of larger areas of shore, and Kitching's observations were particularly connected with the upper parts of the sublittoral zone. In the present instance, each of the areas prepared was comparatively small and surrounded by areas bearing a climax flora and fauna. Recolonization might therefore be expected to proceed more rapidly than in some of the instances cited above. This has actually proved to be the case, as a comparison of the times of appearance and spread of the flora in the present instance with the data given by Moore (**30**) shows. In the latter instance only *Porphyra umbilicalis* and a few *Fucus vesiculosus* had appeared some fourteen months after the preparation of the beach had been completed and fucoids in general were not abundant until two years afterwards, whereas in the present case some algal growth had taken place on each rock (with the exception of rock 4) only three months after preparation and after fifteen months recolonization was in most cases well under way and on rock 3 (Fig. 12) the surface was practically covered. Further, in the circumstances under discussion, recolonization by certain elements of the fauna was due to the migration of mature individuals from surrounding areas, rather than the deposition of larval stages (e.g. *Patella vulgata*, rocks 2 and 6; *Littorina* spp., rocks 1, 3, 4 and 5). The lag in recolonization on the beach described by Moore (**30**) may also partly have been due to its formation from freshly blasted blocks of limestone; on Bardsey any process of 'curing' by sea water would not be necessary. However, wide differences in the rate of recolonization do exist, as Pieron & Huang (**35**) found a very rapid rate of recolonization on the rocky shores of Puget Sound.

The initial appearance of green algae, specifically mentioned in the description of the recolonization of rock 2, but occurring elsewhere where environmental conditions were favourable (rocks 1, 3 and 4, but not rocks 5 and 6) has been emphasized by others (Wilson, Hatton, Kitching and Moore), but it is still difficult to decide whether it represents a stage (in

the successional sense) in the recolonization of a denuded rock or rock area. In the present series the appearance of green and brown algae was (within the limits of the observations made, admittedly at rather long intervals) coincident and, though in some cases the areas covered by green algae were the larger (e.g. rocks 1 and 2, July 1936), the green algae never completely covered the rock surface, later to be replaced by fucoids. Further, in some cases the green algae appeared as a transient stage, later disappearing completely (rocks 2 and 4); in others they persisted throughout the period of the survey (rock 1). Persistence or the reverse seems partly to be correlated with the rate of growth of the brown algae which, in most cases, eventually cover the green algae. As a general conclusion from this examination of recolonization it may be stated that, assuming environmental conditions to be favourable, some growth of green algae will initiate recolonization, but this growth is not extensive and cannot be considered as a 'stage' in recolonization in the sense that its presence is necessary for the later growth of brown algae.

Table 5. *Density of* Patella *populations, rocks 2 and* 6 (Fig. 11)

Date	Rock 2 (*Patella*, numbers per sq. ft.)	Rock 6
April 1936	0·0	0·0
July 1936	1·1	1·5
April 1937	4·6	5·1
July 1937	6·5	6·5
April 1938	9·4	7·0
July 1938	—	6·0

Table 6. *Percentage areas of rock covered with fucoids*, 1936–38 (Fig. 12)

Date	Rock 2	Rock 3	Rock 4	Rock 5
April 1936	—	—	—	—
July 1936	Tr.	3·7	—	3·9
April 1937	31·3	69·8	44·7	4·4
July 1937	39·2	98·2	66·2	8·3
April 1938	66·2	100·0	82·4	10·1
July 1938	97·6	100·0	82·0 (app.)	13·1

Table 7. *Rate of growth of algae, rocks* 1–5, 1937–38 (Fig. 13)

Date	Rock 1 (Average height of algae (cm.))	Rock 2	Rock 3	Rock 4	Rock 5
April 1937	3·4	6·5	7·5	6·0	—
July 1937	8·1	10·1	19·6	10·3	1·0
April 1938	17·0	17·5	42·5	20·1	1·8
July 1938	20·6	18·9	51·8	30·0	2·1

Table 8. *Rate of growth of algae, rocks* 3 *and* 4, 1937–38 (Fig. 14)

Date	Rock 3 *F. serratus* (Average height of algae (cm.))	Rock 3 *F. vesiculosus*	Rock 4 *F. vesiculosus* (overswept)	Rock 4 *F. vesiculosus* (normal)
April 1937	—	—	1·3	6·0
July 1937	13·1	19·6	2·4	10·3
April 1938	21·6	42·5	4·7	20·1
July 1938	34·0	51·8	6·8	30·0

Table 9. *p*H *changes caused by isolated algae* (Fig. 17)

(*a*) Under favourable conditions

Alga	12.30 p.m. (*p*H)	2.25 p.m.	4.50 p.m.	6.15 p.m.	9.30 p.m.
Corallina officinalis	8·3	9·3	9·3	9·3	9·3–9·4
Enteromorpha intestinalis	8·3	9·4–9·5	9·5–9·6	9·6	9·6
Fucus serratus	8·3	8·6–8·7	9·5	9·4–9·5	9·5
Control (sea water)	8·3	8·3–8·4	8·4–8·5	8·3–8·4	8·3–8·4
Temperature (°C.)	22·0	24·5	18·75	17·5	14·0

(*b*) Under unfavourable conditions

Alga	12.0 noon (*p*H)	2.15 p.m.	4.45 p.m.	6.15 p.m.	8.30 p.m.
Corallina	8·3	8·6	8·5–8·6	8·5–8·6	8·7
Enteromorpha	8·3	8·1	8·3–8·4	8·5	8·6
Control (sea water)	8·3	8·3	8·4	8·3–8·4	8·4
Temperature (°C.)	13·0	14·0	13·0	13·0	12·5

The appearance of *Fucus vesiculosus* on rock 4 and *F. vesiculosus* and *F. serratus* on rock 3, though both surrounded by rocks bearing *Ascophyllum nodosum* (and both originally covered with this alga), is also of interest. Many descriptions have been given of the vertical zonation of sea-weeds and theories advanced in its explanation (e.g. Darbyshire (7), Baker

(1, 2), Gail (10, 11), Rees (38), Kitching (22), Wilson (46), Grubb (15), Zaneveld (48), Gibb (12, 13) and many others). In the majority of these descriptions the sequence of zones is *Pelvetia canaliculata*, *Fucus spiralis*, *Ascophyllum nodosum*, *Fucus vesiculosus* and *F. serratus*, but *F. vesiculosus* is also known to have a vertical range greater than that of other species, so that it may occur above, within or below the *Ascophyllum* zone (Wilson, Darbyshire, etc., and noted earlier in this paper), so that its appearance within the *Ascophyllum* zone on rocks 3 and 4 does not involve any extension of its known limits. The two rocks on which this growth occurred are widely separated within the *Ascophyllum* zone (thus having different periods of tidal exposure), and differed also

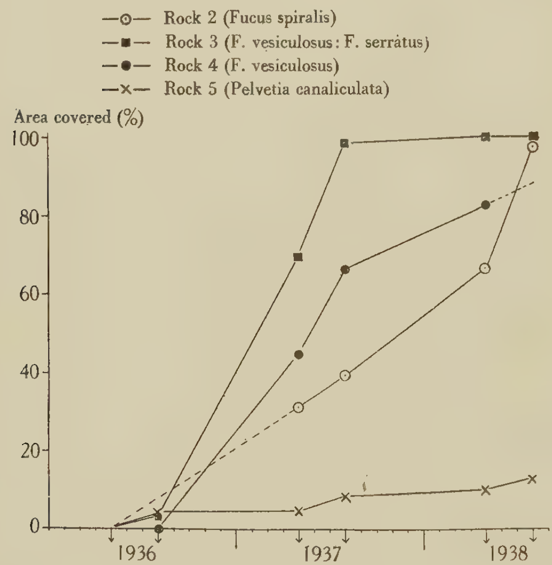


Fig. 12. Percentage areas of rock covered with fucoids, April 1936 to July 1938.

both in their angle of slope and in the form of their surface (see Table 4), so that the appearance of *Fucus vesiculosus* on both would almost suggest that this is a stage in the process of recolonization. If this is so, the sequence of development must be very slow since the flora of both rocks, at the end of the period of survey, had every appearance of stability. In the absence of further evidence and remembering the absence of evidence of sequence in the recolonization of rock surfaces in general (Kitching (23)) an explanation based upon the effect of local environmental factors seems more likely. *Ascophyllum* is recorded as being more prominent on steeply sloping surfaces, whereas *Fucus vesiculosus* and *F. serratus* are more common on horizontal or gently sloping surfaces, so that on both these rocks (in spite of the difference in angle of slope) conditions might be supposed to favour the growth of *F. vesiculosus* rather than *Ascophyllum*. Further, *Fucus vesiculosus* can grow under conditions of greater exposure than *Ascophyllum* (Rees (39), Kitching (22)): denudation of a rock surface will increase the exposure locally, a factor again in favour of *Fucus vesiculosus*. Observations made on the growth rates of fucoids on these rock surfaces (Figs. 13, 14) indicate that *F. vesiculosus* is capable both of rapid growth where environmental conditions are favourable (e.g. rock 3, Fig. 13) and of

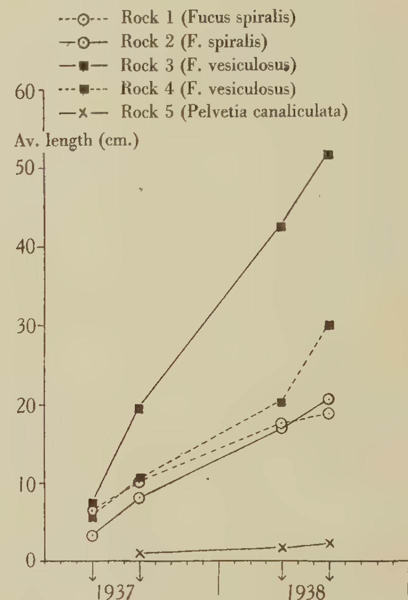


Fig. 13. Rate of growth of algae. Rocks 1–5, April 1937 to July 1938.

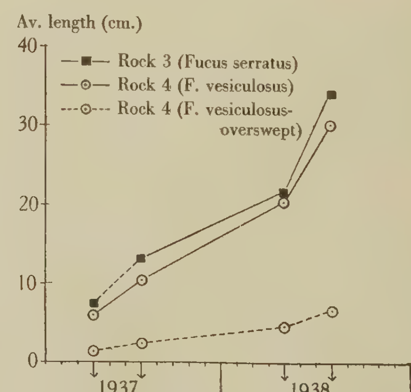


Fig. 14. Rate of growth of algae. Rocks 3 and 4, April 1937 to July 1938.

attachment and growth (though at a reduced rate) where conditions are less favourable (e.g. rock 4, Figs. 13, 14, where the period of submergence is less and where, over part of the rock at least, the surface is swept by the fronds of the surrounding *Ascophyllum*).

The complete nature of the replacement of *Ascophyllum* by *Fucus* spp. on these two rocks, producing a sharp boundary between the recolonized areas and those surrounding them, suggests a comparison with the sharp boundaries recorded as existing normally between adjacent zones (Colman (5), Grubb (15)). Many investigators have suggested factors which may control the zonation of algae (these factors have recently been summarized by Chapman (4), pp. 349–51), but the mode of action of any one of these factors would appear to be gradual so that there is an optimum condition, operating over a limited area, with areas where conditions are less favourable on either side [e.g. *Fucus spiralis* can tolerate exposures varying from 94 to 38·8%, but maximum growth occurs where the exposure lies between 89 and 75·7% (Grubb (15)): the growth of *Fucus* is severely inhibited if the *p*H of the water is greater than 8·4 and 'almost completely inhibited' above 8·6 (Gail (11))]. The effect of a single factor would not be likely, therefore, to produce the sharp zonal boundaries which actually occur. Since it is possible to envisage the factors which have produced, under the artificial conditions operating in the process of recolonization, sharp boundaries between the areas recolonized and those around, an explanation of the general sharpness of definition of the zonal boundaries (which applies both to plants and animals of the littoral zone, Colman (5)) in terms of the interaction of several factors would appear to offer better chances of success. The study of this interaction would not be easy, especially in the light of the suggestion put forward by Moore & Sproston (31) that, if any individual is living under conditions unfavourable in one respect, its resistance to other environmental conditions is lowered.

Opinions differ as to the intensity of competition occurring during the process of recolonization. Kitching (23) and Moore (30) have both commented on the lack of intense competition during this process, but Moore & Sproston (31) state that this stage is followed by one in which competition is more severe. Rees (40) has emphasized competition that may occur between the pioneer algae colonizing wood and concrete and later arrivals, and with certain marine animals and under the conditions described by Pieron & Huang (35) competition must be intense. In the present instance, no severe competition seems to be suggested by the rate and type of recolonization that has taken place.

4. THE ROCK-POOL ENVIRONMENT

Though several investigations have been made of isolated aspects of the non-biotic factors in the rock-pool environment (e.g. Powers (36), Johnson & Skutch (19), Humphrey & Macy (18), Biebl (3)) records of more extensive investigations are few. Klugh (24) investigated the effect of a series of environmental factors controlling the biota of rock pools and came to the conclusion that temperature was the most important limiting factor and Stephenson, Zoond & Eyre (43) have studied the variations in oxygen content and *p*H values of a series of rock pools in the Cape Peninsula, South Africa, but otherwise there is little detailed information of the diurnal variation, or of variations over longer periods, of the environmental factors of such pools.

In order to investigate these factors more fully, a detailed study of their variation in a series of five pools, situated on the west, south-west and south-east coasts of the island, was made. The lowest of these pools were situated at about mid-tide level and the highest just above high-water mark of spring tides. Isolated readings made on other pools indicated that those selected represented typical conditions over this part of the littoral zone. Attention was concentrated on these pools in the upper half of the littoral zone because these should show something of the maximum environmental rigour to which the pool flora and fauna is subjected.

Table 10. *Physical features of rock pools*

No.	Dimensions m.	Max. depth m.	Av. depth m.	Tidal level	Degrees of shade
3	8·7 × 5·1	0·55	0·23	Just above H.W.M.S.T.	Slight
6	6·6 × 10·5 × 11·3	0·50	0·23	Above mid-tide level	None
7	15·6 × 6·6	0·43	0·18	Above H.W.M.S.T.	Some
10	5·8 × 1·15	0·64	0·25	Between H.W.N. and H.W.S.	None
14	4·45 × 1·3	1·29	0·42	Above mid-tide level	Some

(*a*) *Description of the pools*

The chief physical features of these pools are summarized in Table 10 above; their positions are shown in Fig. 1.

The full list of the fauna and flora of these pools is given in Appendix 1, but the following description of the pools studied is given to supplement the discussion of the effects of the environmental factors.

Pool 3 is a shallow pool, rectangular in outline, with an uneven floor of large and small stones: some of the larger boulders project out of the water. The latter were fringed with *Enteromorpha intestinalis* (which also covered the floor in the shallowest bays) and the submerged stones were partly covered with *Chaetomorpha linum*, *C. tortuosa* and *Cladophora*. The fauna was scanty, chiefly amphipods (*Amphithoë*

rubricata and *Melita palmata*) and *Littorina saxatilis*. Sea water entered at the higher spring tides, and conditions between these periods were made more extreme from time to time by plant debris (chiefly *Laminaria* stalks and fronds) which was washed in.

Pool 6 had a denser and more varied fauna and flora than pool 3. The floor was of large stones and shingle, and sand with small stones, each type covering about half the area of the floor. The larger stones at the deeper end were fringed with *Ascophyllum nodosum* and the smaller stones in the shallower areas carried *Enteromorpha intestinalis*. Other algae, green, brown and red, occurred in patches. Polychaetes, Molluscs and Crustacea were the commonest members of the fauna. The pool was in contact with the sea for periods up to four hours during each tidal period.

Pool 7 represented the most extreme conditions investigated, since sea water only entered in quantity during south-west gales, though some spray would enter at ordinary spring tides. The floor was of boulders and stones, the latter sometimes fringed with *Enteromorpha intestinalis*. The fauna was much reduced, though *Jaera marina* and *Procerodes ulvae* were locally common.

the denser masses of algal growth (small specimens of *Perinereis cultrifera*, *Amphithoë rubricata* and *Naesa bidentata*, *Asterina gibbosa*), and *Patella vulgata* (which occurred on the steep sides of the pool, usually just above water level) was also present.

Temperature, hydrogen-ion concentration, oxygen and chloride content were measured in these pools. The hydrogen-ion concentration was determined colorimetrically, using a B.D.H. comparator, the oxygen content by Winkler's method and the chloride content by Mohr's method. Titration against standard silver nitrate for the determination of chloride was carried out after returning to the mainland, all other determinations being carried out on the island. Allowance was made for the chloride content in calculating the percentage saturation values, in terms of which the oxygen concentrations are expressed. The significant results of these studies are shown in Fig. 15 (oxygen content) and Fig. 16 (*p*H), and the detailed readings are given in Appendix 2.

(*b*) *Discussion of results*

These investigations had necessarily to be made on different days, so that the results obtained are not strictly comparable but, as is shown in Table 11 above, the differences in atmospheric conditions were insufficient to affect the main implications of the results obtained.

Table 11. *Temperature ranges during diurnal readings of rock pools*

Pool no.	Air temperature (°C.)			Surface-water temperature (°C.)		
	Min.	Max.	Diff.	Min.	Max.	Diff.
3	13·75	26·25	12·5	15·5	22·0	6·5
6	14·25	23·0	8·75	14·0	19·25	5·25
7	13·75	23·75	10·0	13·5	23·0	9·5
10	14·0	22·5	8·5	13·0	19·0	6·0
14	17·75	26·0	8·25	15·5	20·75	5·25

Pool 10 is part of a V-shaped cleft running up from the sea in which conditions were, in some respects, intermediate between those obtaining in pool 3 and those in pools 6 and 14. Sea water entered regularly at the spring tides. *Cladophora* formed a dense growth over much of the steep, rocky sides of the pool and there was a fringe of *Enteromorpha intestinalis*, more extensive in the shallower areas. *Clavelina lepadiformis* occurred in some numbers. The floor was rocky, with some stones.

Pool 14, situated approximately at the same tidal level as pool 6, was chosen principally because of the density of its flora. The floor was rocky, with some larger boulders, the sides rocky and steep. The whole of the sides and much of the floor was covered with *Lithothamnion* sp. (? *lichenoides*), associated with *Corallina officinalis*, with an overlying flora of *Enteromorpha compressa* and *Cladophora*. Patches of *Myrionema strangulans* and *Pterocladia capillacea* were common and there was some *Chondrus crispus*. The larger brown algae were only poorly represented—there was a single plant of *Fucus serratus* and a patch of tattered *Laminaria digitata*. The fauna was comparatively poor—some forms were associated with

The most important factor governing the variations in oxygen concentration or *p*H value is clearly the density of the flora. This has already been pointed out by several investigators and studied in some detail by Stephenson *et al.* (**43**). Figs. 15 and 16 show the range of variation that would be expected. Pool 14, with a dense flora and relatively scanty fauna, shows a considerable degree of supersaturation (the maximum figure of 271 % is practically the same as that recorded by Orr (**33**) in coral pools) with a correspondingly high *p*H value (9·3 for a period of over two hours), whereas in pool 7, with the most scanty flora, the maximum *p*H value was 8·5, with an oxygen maximum of 122 % saturation. The values for the other pools lie between these extremes. Even in pool 7, however, there was an appreciable rise in the oxygen content of the water (from 71·5 to 122 % saturation) and some increase in *p*H (8·3–8·5). The cause of these variations is not altogether clear. The amount of *Enteromorpha* in

pool 7 was small, and tests made on sealed samples of water did not show any significant changes of pH.

It was thought possible that the composition of the rock-pool flora might be of some importance in influencing the range of these diurnal changes. The following rough experiments were carried out in order to test this possibility. Known (wet) weights of alga were placed in tubes, completely filled with sea water and then sealed, these being then exposed,

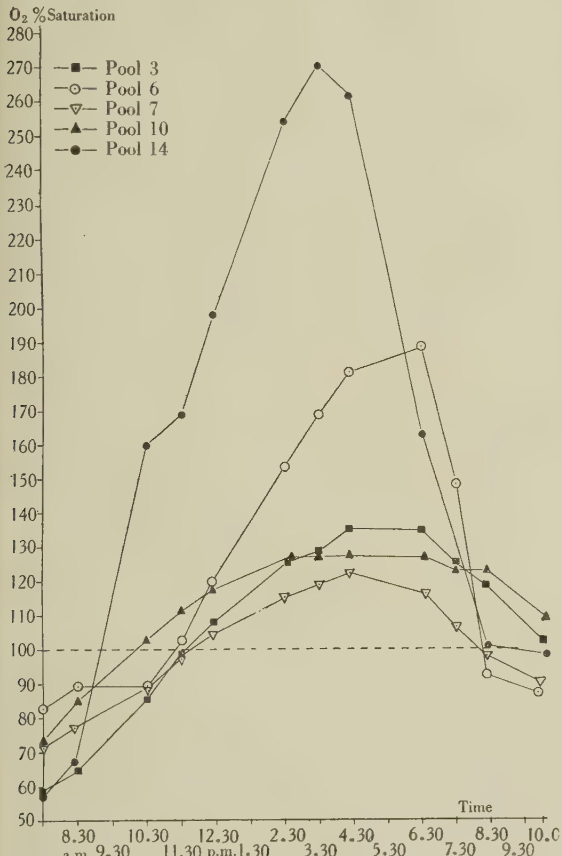


Fig. 15 (see Appendix 2 *a*). Diurnal changes in oxygen content (July).

immersed in a water bath, for some hours. Samples were removed for estimation of pH at intervals during this period. The results of typical experiments, both under favourable and less favourable environmental conditions, are shown in Fig. 17, and do not indicate that there is any important difference between the algae compared (other common pool algae were used in other experiments, but the results obtained were very much the same as those given in Fig. 17). Thus the composition of the flora would seem to have little importance as a major factor, a conclusion which is supported by readings made on other pools on the shore, in cases where the flora was almost entirely composed of one particular species of alga. All these isolated readings, both of oxygen content and pH value, fell within the range described above.

In those pools situated between tide marks, periodic contact with the sea has a levelling effect on

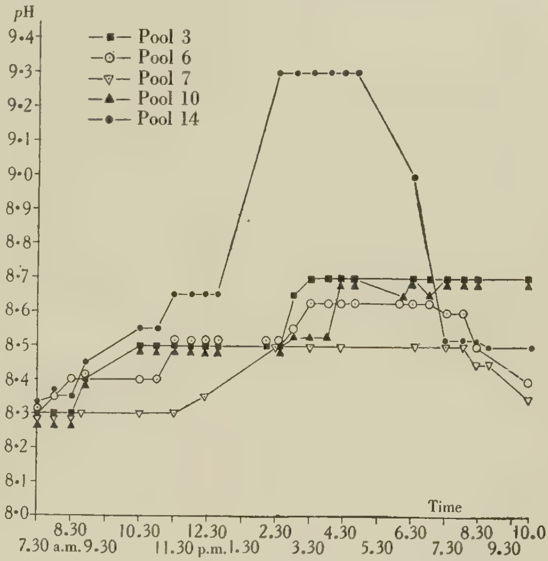


Fig. 16 (see Appendix 2 *a*). Diurnal changes in hydrogen-ion concentration (July).

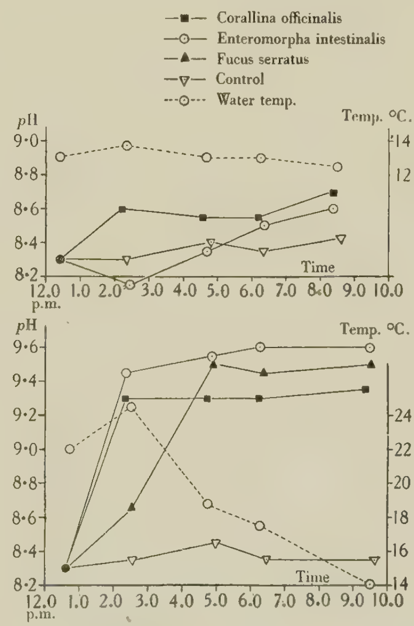


Fig. 17. pH changes caused by isolated algae.

the diurnal changes, so that such pools have a smaller range of daily variations than others not in such regular contact. The time of contact is clearly of importance; contact during the middle of the day should reduce the oxygen content and the pH value,

at other times the effect of this contact should, presumably, be less. Figs. 18 and 19 summarize the results obtained from two series of diurnal readings of pool 6, one with an early morning high tide (the pool was in contact with the sea from 7.30 to 10.45 a.m. and the evening from 7·30 p.m. onwards), the other with a mid-day high tide (contact being established from approximately 12.45 to 4.45 p.m.), carried out in an attempt to assess the effect of variation in time of contact. In both cases there was, of course, a marked effect on the diurnal temperature changes (Fig. 18), but the effects on the oxygen and *p*H, though discernible, were less marked. With the mid-day high tide both continued to rise, though, in the case of oxygen concentration, less rapidly than before. It seems likely that the form of the shore in the immediate vicinity of the pool, in determining the way in which water enters, would be of more importance in causing marked changes in the diurnal rhythm than the time of contact. If the water enters rapidly and boisterously, complete mixing would be more immediate, and the effect on the environment more marked than in the present instance.

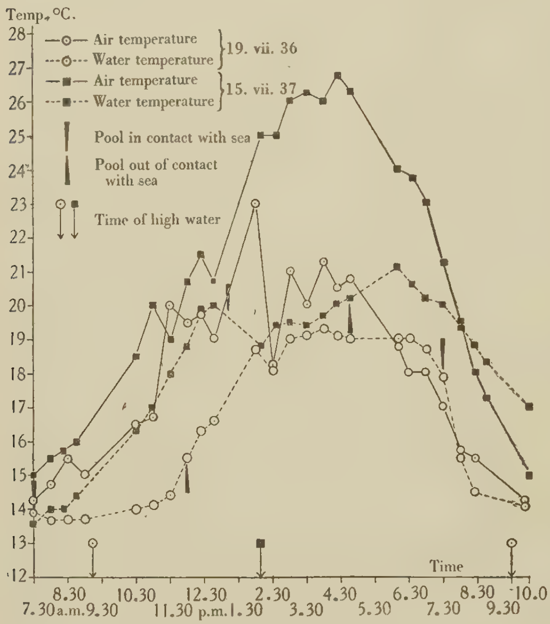


Fig. 18. Diurnal temperature changes, pool 6, July 1936 and July 1937.

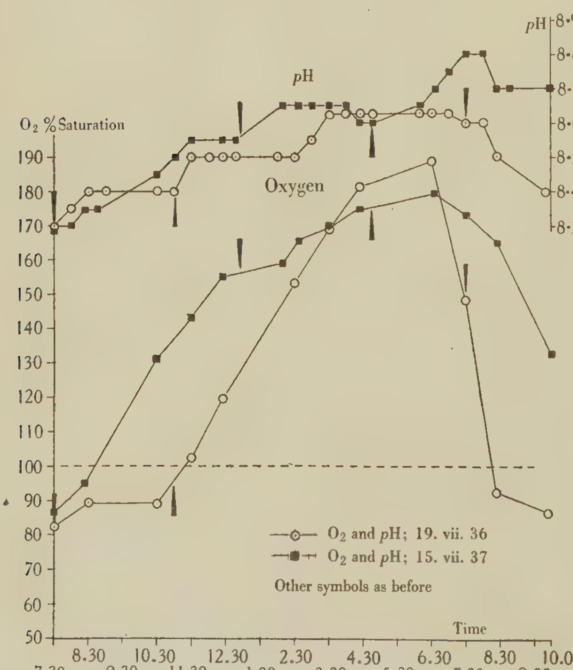


Fig. 19. Diurnal changes in oxygen content and *p*H, pool 6, July 1936 and July 1937.

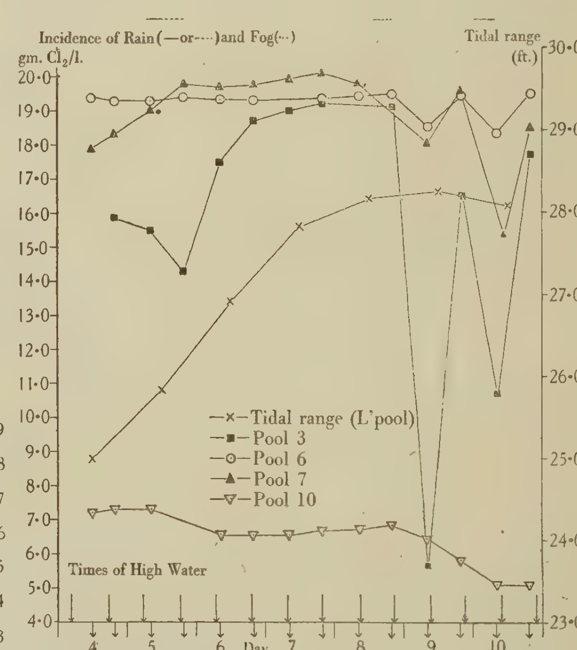


Fig. 20. Daily changes in salinity, pools 3, 6, 7 and 10, July 1937.

Determinations of the chloride content of pools 3, 6 and 10 for weekly periods indicate other factors and their effect on the pool environment. Fig. 20 shows a series of such readings made in July 1937. During this week there were two periods of heavy rain, one at the beginning, just before the spring tidal period and one later, which coincided with the spring tides. The earlier period of rain had no apparent effect on the chloride content of pool 6, though the salinity of both pools 3 and 10 were decreased. The salinity of these pools once more increased towards the middle of the week. The later period of rain had some effect on pool 6, where some alternation of increased and decreased salinity

occurred, and had a profound effect on the salinity of pool 3, where variations comparable with those recorded under estuarine conditions occurred. These marked fluctuations, though chiefly affecting the surface water, do also affect the deeper water (see below) and thus must restrict the fauna of such pools. Some of the species in pool 3 (e.g. *Littorina saxatilis*) are known to be able to live in water of reduced salinity (Gowanloch & Hayes (14)). The chloride content of pool 7, out of contact with the sea throughout the period, was initially much lower than that of the other pools and had decreased markedly by the end of the week.

These results may be compared with those obtained during the April spring tides the following year (Fig. 21). No marked fluctuations occurred, but

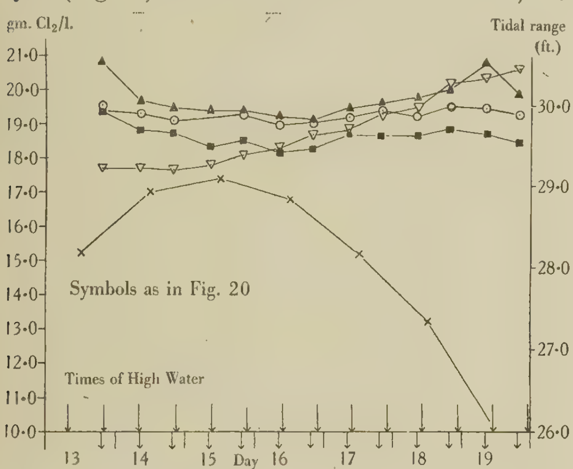


Fig. 21. Daily changes in salinity, pools 3, 6, 7 and 10, April 1938.

the chloride content of pool 7 increased steadily during this period of fine weather. A comparison of the salinities recorded earlier in this pool and those shown in Fig. 21 indicates something of the rigour of this environment: animals living in such pools must not only be capable of living in water which has wide variation in salinity, but must also be capable of withstanding prolonged periods of low or high salinity. Fig. 22, based upon readings made in July 1938, shows the effect of rain upon the surface and deeper water of pools 3 and 10. During this period, pool 10 was periodically in contact with the sea, and the salinity quickly became uniform, but in pool 3, which was not in contact, the effects of heavy rainfall early in the week were more persistent, though the salinity gradually became more uniform.

Figs. 23 and 24 give the results obtained from a series of daily readings of oxygen content and *p*H value, made on pools 3, 6 and 10. These readings are intended partly to supplement the diurnal readings described earlier and partly to indicate the range of variation in these factors over a short period. These readings were made between 10.0 and 11.0 a.m. and 6.0 and 7.0 p.m., the pools being visited in the same sequence (6, 3, 10) each time observations were made. Temperature readings were also made and showed that in the tidal pool (6) the water temperature was invariably below that of the air, whereas in pools 3 and 10 the reverse relationship, in general, occurred. Although differences in salinity between the surface and bottom water persisted throughout the period under review in pool 3 (see section above), there was no evidence, from the temperature readings, of any layering of the water. The differences in temperature between the surface and the bottom were quite irregular and could not be correlated with salinity differences or with tidal effects. Day to day

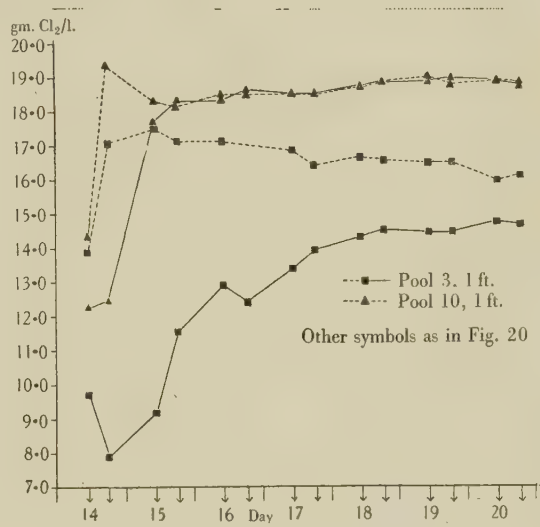


Fig. 22. Daily changes in salinity, pools 3 and 10, July 1938.

variation in the air temperature was the controlling factor of the water temperature.

The diurnal variation in oxygen content (Fig. 23) shows that the water of these pools may generally be supposed to be supersaturated with oxygen during daytime in the summer. The range of variation recorded is generally within that observed earlier in the more detailed readings; pool 6 showed the greatest daily range of the series (101·7%), and the average daily variation of this pool (62·5%) is greater than that of pool 10 (38·6%) and pool 3 (35·4%), a difference which emphasizes the greater importance of floral content than tidal level. This is also reflected in the degree of difference between the three pools in the evening readings on successive days; these differences were greatest when environmental conditions were most favourable for photosynthesis. On these occasions the gross differences between the pool with the densest flora (pool 6) and that with a less dense flora (pool 10) were surprisingly constant (54, 51 and 54%), though this correspondence would seem largely a matter of chance.

The most striking features of the daily variation in *p*H value (Fig. 24) were the regular rhythm in the readings for pool 6 and the somewhat anomalous conditions, occurring towards the end of the period, in the other two pools. Pool 10 showed some diurnal rhythm throughout, but the values recorded increased at a fairly steady rate all the time, and in pool 3

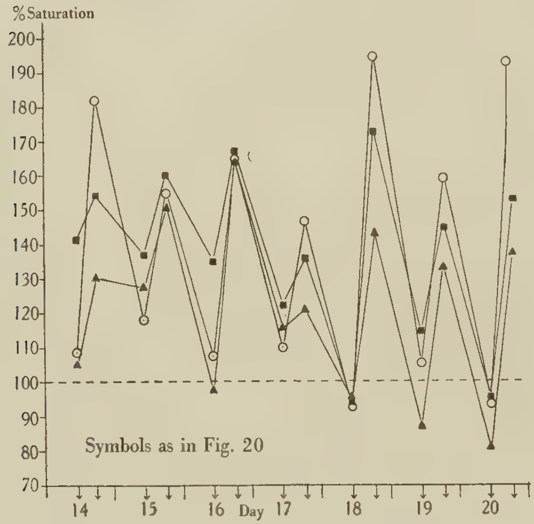


Fig. 23. Daily changes in oxygen content, pools 3, 6 and 10, July 1938.

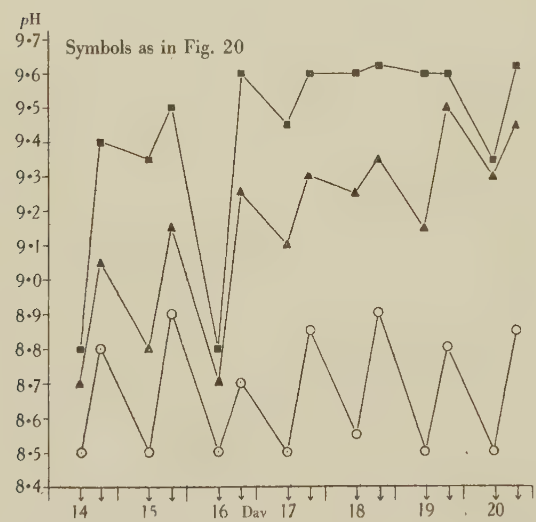


Fig. 24. Daily changes in *p*H, pools 3, 6 and 10, July 1938.

a marked diurnal rhythm earlier in the week gave place to more uniform, high values later. These later conditions in pools 3 and 10 have no counterpart in the daily oxygen changes, and it is difficult to suggest their cause. As the daily rhythms in *p*H values were more normal at those times when these pools were in contact with the sea (at least in the case of pool 10), the anomalous conditions observed later may in part be an outcome of isolation.

5. SUMMARY

1. An account is given of the shore fauna of Bardsey Island. Much of this shore is exposed, with a consequent reduction in the diversity of the fauna, though comparisons with records of areas investigated in Cardigan Bay indicate that the littoral fauna is fairly representative. A list of the fauna is given.

2. A more detailed account is given of investigations made of the recolonization of bared rock surfaces and of the environmental factors of rock pools.

3. The initial stages in the recolonization of rock surface are characterized by the appearance of green algae (particularly *Ulva* and *Cladophora*) except in the case of the most exposed surface, where there was some growth of *Porphyra*. This initial growth only covered a small proportion of the rock surface and usually soon disappeared, to be followed by a more extensive and more permanent growth of fucoids (again with the exception of the most exposed surface, where there was a more transient fucoid growth). This later growth, though more rapid on rocks nearer low-water mark, was gradual and did not suggest intense competition for the area exposed. In two cases the flora of the rock was different from that of adjacent areas. The causes of this difference, and their bearing on the zonation of fucoids in general, are discussed.

4. The rock-pool environment has been studied by a series of diurnal readings, supplemented by daily readings over longer periods. Oxygen concentration, *p*H, chloride content and temperature were recorded. The density of the flora is the most important factor governing the range of oxygen and *p*H variations: so far as observations and experiments have been made, the particular species of alga present has little influence.

5. Daily readings indicate a fairly regular rhythm in pools situated between tide marks, but a less regular series of changes in those near high-water mark. The salinity of such pools may also vary widely, particularly if a spring tidal period coincides with heavy rain. Under these circumstances fluctuations comparable with those recorded under estuarine conditions may occur in the chloride content, these being most marked at the surface, but also affecting the deeper water. Recovery from such conditions may take several days. The salinity of pools above high-water mark spring tides also varied considerably, but the variations were more gradual and periods of high or low salinity more prolonged. The diurnal changes of tidal pools are only slightly affected by the time during which contact with the sea occurs: it is suggested that the configuration of the neighbouring shore, with its effect on the way in which water enters the pool, may be a factor of some importance.

6. ACKNOWLEDGEMENTS

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by a grant made by the Council of University College, Nottingham. Grateful acknowledgement is made for this financial assistance. I also wish to express my thanks to Miss D. Bexon for her help in identifying the algae; and to all those people, both on Bardsey Island and on the adjoining mainland, who so readily helped in the transport of material and apparatus.

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APPENDIX I. FLORA AND FAUNA OF THE ROCK POOLS

(*Species authorities already listed in Table 2 are omitted.*)

Pool 3

CHLOROPHYCEAE
- Enteromorpha ramulosa Hook.
- E. intestinalis Link.
- Chaetomorpha tortuosa Kütz.
- C. linum Kütz.
- Cladophora rupestris Kütz.
- Cladophora sp.

RHODOPHYCEAE
- Chondrus crispus Stackh.
- Ceramium rubrum Ag.

PORIFERA
- Hymeniacidon sanguinea

CRUSTACEA
- Melita palmata (Montagu)
- Amphithoë rubricata
- Carcinus maenas

INSECTA, Diptera
- Cricotopus fucicola Edwards

Pool 6

CHLOROPHYCEAE
- Enteromorpha ramulosa
- E. intestinalis
- Ulva lactuca L.

PHAEOPHYCEAE
- Scytosiphon lomentarius J. Ag.
- Asperococcus fistulosus Hooker
- Myriotricha filiformis Harv.
- Fucus spiralis L.
- Ascophyllum nodosum Le Jol.
- Pelvetia canaliculata Dene & Thur.

RHODOPHYCEAE
- Chondrus crispus
- Plocamium coccineum Lyngb.*
- Polysiphonia fastigiata Grev.
- Corallina virgata
- Ceramgium rubrum
- Furcellaria fastigiata Lamour

LICHENES
- Catenella opuntia

PORIFERA
- Leucosolenia botryoides
- Sycon ciliatum
- Adocia cinerea
- Hymeniacidon sanguinea

COELENTERATA
- Obelia geniculata*
- Halicornaria (Aglaophenia) pennatula (Ellis & Solander)*
- Aurelia aurita (Linné)
- Actinia equina

ANNELIDA
- Harmothoë spinifera
- Perinereis cultrifera
- Lanice conchilega (Pallas)
- Pomatoceros triqueter
- Spirorbis borealis
- Marionina semifusca

CRUSTACEA
- Leander squilla (Linné)
- Eupagurus bernhardus
- Carcinus maenas

MOLLUSCA
- Patella vulgata
- Gibbula cineraria
- G. umbilicalis
- Littorina saxatilis
- L. littoralis
- L. littorea

POLYZOA
- Membranipora pilosa*

* Indicates washed in.

Echinodermata
- Asterina gibbosa
- Amphipolis squamata

Tunicata
- Botryllus schlosseri
- Amaroucium proliferum*

Teleostei
- Spinachia vulgaris Fleming

Pool 7

Chlorophyceae
- Enteromorpha intestinalis

Platyhelminthes
- Procerodes ulvae

Crustacea
- Jaera marina
- Gammarus sp. (? chevreuxi Sexton)

Mollusca
- Littorina saxatilis

Pool 10

Chlorophyceae
- Enteromorpha intestinalis
- Chaetomorpha aerea Kütz.
- Cladophora rupestris

Rhodophyceae
- Plocamium coccineum

Porifera
- Leucosolenia botryoides
- Halichondria panicea*

Coelenterata
- Halicornaria (Aglaophenia) pennatula
- Bunodactis verrucosa

Annelida
- Spirorbis borealis

Crustacea
- Tanais cavolini
- Gammarus sp.

Mollusca
- Cingula semicostata
- Aplysia punctata

Polyzoa
- Cellepora pumicosa Linné*
- Crisia denticulata (Lamarck)*
- Stomatopora major (Johnston)*
- Lichenopora hispida (Fleming)*

Tunicata
- Clavelina lepadiformis (O. F. Müller)

Pool 14

Chlorophyceae
- Enteromorpha compressa Grev.
- Cladophora sp.

Phaeophyceae
- Myriotricha filiformis
- Sphacelaria cirrhosa Ag.
- Myrionema strangulans Grev.
- Laminaria digitata Lamour
- Fucus serratus L.

Rhodophyceae
- Pterocladia capillacea Born.
- Gelidium corneum Lamour
- Chondrus crispus
- Furcellaria fastigiata
- Lithothamnion sp.? lichenoides Fosl.
- Corallina officinalis L.

Coelenterata
- Actinia equina
- Sagartia sp.

Annelida
- Ferinereis cultrifera

Crustacea
- Naesa bidentata
- Amphithoë rubricata

Mollusca
- Patella vulgata

Echinodermata
- Asterina gibbosa

* Indicates washed in.

APPENDIX 2. MEASUREMENTS OF ENVIRONMENTAL CONDITIONS IN THE ROCK POOLS

(a) Diurnal series

Pool 3. 21 July 1936. High water 10.10 a.m., 10.35 p.m.

Time	Air temp. ° C.	Water temp. ° C. Surface	Water temp. ° C. Bottom	Oxygen % sat.	pH	Chloride g./l.
7.30 a.m.	13·75	—	15·6	58·9	8·3	—
8.0 a.m.	14·25	—	15·6	—	8·3	—
8.30 a.m.	15·0	—	15·8	64·4	8·3	—
8.50 a.m.	15·5	—	15·8	—	8·4	—
10.30 a.m.	18·5	—	17·3	85·6	8·5	—
11.0 a.m.	17·75	—	17·5	—	8·5	18·7
11.30 a.m.	20·5	18·6	18·0	99·1	8·5	—
12.0 noon	22·0	19·4	18·7	—	8·5	—
12.25 p.m.	22·75	20·2	19·4	108·8	8·5	—
12.45 p.m.	23·0	20·4	19·7	—	8·5	—
2.15 p.m.	25·75	21·8	20·8	—	8·5	18·73
2.35 p.m.	24·25	21·9	21·2	125·9	8·5	—
3.0 p.m.	25·25	22·2	21·3	—	8·6–8·7	—
3.30 p.m.	23·5	22·2	21·8	129·4	8·7	—
4.0 p.m.	23·25	22·2	21·9	—	8·7	—
4.25 p.m.	26·25	22·5	21·9	135·8	8·7	18·8
4.45 p.m.	26·25	22·6	21·9	—	8·7	—
6.10 p.m.	21·0	22·2	21·9	—	8·7	—
6.30 p.m.	20·0	22·0	21·9	135·0	8·7	—
7.0 p.m.	19·5	21·8	21·6	—	8·7	—
7.30 p.m.	18·0	21·3	21·3	125·9	8·7	18·84
8.0 p.m.	17·75	20·8	20·8	—	8·7	—
8.25 p.m.	17·25	20·6	20·5	118·7	8·7	—
9.55 p.m.	16·0	19·7	19·7	102·6	8·7	18·98

Pool 6. 19 July 1936. High water 9.17 a.m., 9.30 p.m.

Time	Air temp. ° C.	Water temp. ° C. Surface	Water temp. ° C. Bottom	Oxygen % sat.	pH	Chloride g./l.
6.30 a.m.	13·75	13·3	—	61·2	8·1	19·19
7.0 a.m.	13·50	13·3	—	—	8·3	19·3
*7.30 a.m.	14·25	13·9	—	82·4	8·3	19·33
*8.0 a.m.	14·75	13·7	—	—	8·3–8·4	—
*8.30 a.m.	15·5	13·7	—	89·6	8·4	19·37
*9.0 a.m.	15·0	13·7	—	—	8·4	—
*10.30 a.m.	16·5	14·0	—	89·4	8·4	—
*11.0 a.m.	16·75	14·1	—	—	8·4	19·4
*11.30 a.m.	20·0	14·4	—	102·2	8·5	—
12.0 noon	19·5	15·5	—	—	8·5	—
12.25 p.m.	19·75	16·3	—	119·9	8·5	—
12.45 p.m.	19·0	16·6	—	—	8·5	19·4
2.0 p.m.	23·0	18·7	—	—	8·5	—
2.30 p.m.	18·25	18·1	—	153·8	8·5	—
3.0 p.m.	21·0	19·0	—	—	8·5–8·6	19·37
3.30 p.m.	20·0	19·1	—	168·9	8·6+	—
4.0 p.m.	21·25	19·3	—	—	8·6+	—
4.25 p.m.	19·5	19·1	—	181·7	8·6+	—
4.45 p.m.	19·75	19·0	—	—	8·6+	—
6.10 p.m.	18·75	19·0	—	—	8·6+	—
6.30 p.m.	18·0	19·0	—	189·0	8·6+	—
7.0 p.m.	18·0	18·7	—	—	8·6+	19·4
*7.30 p.m.	17·0	17·9	—	148·2	8·6	—
*8.0 p.m.	15·75	15·5	—	—	8·6	19·4
*8.25 p.m.	15·5	14·5	—	92·7	8·5	—
*9.50 p.m.	14·25	14·1	—	86·9	8·4	19·4

* Indicates contact with sea.

Pool 6. 15 July 1937. High water 2.06 p.m.

Time	Air temp. °C.	Water temp. °C. Surface	Bottom	Oxygen % sat.	*p*H	Chloride g./l.
7.0 a.m.	14·25	13·3	13·3	—	8·3	19·23
7.30 a.m.	15·0	13·6	13·4	86·6	8·3	—
8.0 a.m.	15·5	14·0	13·6	—	8·3	19·28
8.25 a.m.	15·75	14·0	13·7	95·3	8·3–8·4	—
8.45 a.m.	16·0	14·4	14·0	—	8·3–8·4	—
10.30 a.m.	18·5	16·3	15·2	131·6	8·4–8·5	—
11.0 a.m.	20·0	17·0	15·5	—	8·5	19·30
11.30 a.m.	19·0	18·0	16·6	143·4	8·5–8·6	—
12.0 noon	20·75	18·8	17·3	—	8·5	—
12.25 p.m.	21·5	19·7	17·9	155·2	8·5–8·6	—
12.45 p.m.	20·75	20·0	18·1	—	8·5–8·6	19·44
*2.10 p.m.	25·0	18·8	18·3	159·0	8·6–8·7	19·42
*2.35 p.m.	25·0	19·4	18·7	165·8	8·6–8·7	—
*3.0 p.m.	26·0	19·5	18·7	—	8·6–8·7	19·42
*3.30 p.m.	26·25	19·4	18·4	169·8	8·6–8·7	—
*4.0 p.m.	26·0	19·7	18·4	—	8·6–8·7	—
*4.25 p.m.	26·75	20·0	18·6	174·7	8·6	—
*4.45 p.m.	26·25	20·2	18·8	—	8·6	19·51
6.10 p.m.	24·0	21·1	19·5	—	8·6–8·7	—
6.35 p.m.	23·75	20·6	19·7	179·5	8·7	—
7.0 p.m.	23·0	20·2	19·5	—	8·7–8·8	19·42
7.30 p.m.	21·25	20·0	19·4	173·5	8·8	—
8.0 p.m.	19·5	19·4	19·0	—	8·8	—
8.25 p.m.	18·0	18·8	18·8	165·3	8·7	—
8.45 p.m.	17·25	18·3	18·4	—	8·7	19·44
10.0 p.m.	15·0	17·7	17·0	132·7	8·7	19·49

Pool 7. 29 July 1936

Time	Air temp. °C.	Water temp. °C. Surface	Bottom	Oxygen % sat.	*p*H	Chloride g./l.
7.10 a.m.	13·5	13·4	13·4	—	8·2–8·3	21·93
7.35 a.m.	13·75	13·6	13·6	71·5	8·3	—
8.0 a.m.	14·25	13·6	13·6	—	8·3	—
8.25 a.m.	14·5	13·7	13·7	77·1	8·3	—
8.45 a.m.	14·25	13·7	13·7	—	8·3	22·0
10.30 a.m.	16·0	14·7	14·7	88·4	8·3	—
11.0 a.m.	16·0	14·7	14·7	—	—	—
11.30 a.m.	18·75	15·9	15·8	98·4	8·3	—
12.0 noon	19·5	17·3	16·9	—	—	—
12.25 p.m.	20·75	18·1	17·9	104·7	8·3–8·4	22·08
12.45 p.m.	21·25	18·8	18·6	—	—	—
2.30 p.m.	21·5	21·8	21·8	115·4	8·5	—
3.0 p.m.	20·0	22·3	22·0	—	—	—
3.30 p.m.	23·75	22·5	22·5	119·1	8·5	—
4.0 p.m.	23·75	22·9	22·6	—	—	22·28
4.25 p.m.	23·0	22·9	22·6	122·2	8·5	—
4.45 p.m.	22·75	22·9	22·9	—	—	—
6.10 p.m.	21·0	21·8	21·5	—	—	—
6.35 p.m.	20·5	21·5	21·3	116·1	8·5	—
7.0 p.m.	19·75	20·9	21·1	—	—	22·46
7.30 p.m.	18·25	20·4	20·4	106·2	8·5	—
8.0 p.m.	17·25	19·5	19·7	—	8·5	—
8.25 p.m.	16·0	19·0	19·1	98·0	8·4–8·5	—
8.45 p.m.	15·25	18·4	18·7	—	8·4–8·5	—
9.55 p.m.	14·5	17·3	17·5	90·2	8·3–8·4	22·50

* Indicates contact with sea.

Pool 10. 25 July 1936. High water 12.55 p.m.

Time	Air temp. ° C.	Water temp. ° C. Surface	Bottom	Oxygen % sat.	pH	Chloride g./l.
7.0 a.m.	13·25	12·7	12·7	—	8·3	19·51
7.30 a.m.	14·0	12·9	13·0	73·8	8·3	—
8.0 a.m.	14·75	13·4	13·1	—	8·3	—
8.25 a.m.	15·75	13·9	13·4	85·2	8·3	—
8.45 a.m.	16·0	14·3	13·4	—	8·4	19·47
10.30 a.m.	19·25	15·9	15·1	102·7	8·5	—
11.0 a.m.	20·0	16·2	15·4	—	8·5	—
11.30 a.m.	21·25	17·6	15·9	111·3	8·5	—
12.0 noon	21·0	18·4	16·3	—	8·5	—
12.25 p.m.	21·75	18·0	16·9	117·8	8·5	19·51
12.45 p.m.	22·5	18·3	17·3	—	8·5	—
2.40 p.m.	21·75	20·2	18·8	127·3	8·5	—
3.5 p.m.	21·5	20·6	19·0	—	8·5+	19·58
3.30 p.m.	20·5	20·2	19·0	127·5	8·5+	—
4.0 p.m.	19·0	19·7	19·1	—	8·5+	19·58
4.25 p.m.	19·5	19·7	19·0	127·9	8·7	—
4.45 p.m.	19·0	19·7	19·0	—	8·7	—
6.15 p.m.	17·75	19·1	18·7	—	8·6–8·7	—
6.35 p.m.	17·75	18·8	18·7	126·9	8·7	—
7.0 p.m.	16·75	18·7	18·6	—	8·6–8·7	19·58
7.30 p.m.	16·5	18·4	18·3	123·6	8·7	—
8.0 p.m.	15·75	18·0	18·1	—	8·7	—
8.25 p.m.	15·75	17·9	17·9	123·6	8·7	—
8.45 p.m.	15·5	17·7	17·7	—	8·7	—
10.5 p.m.	14·25	17·0	17·3	109·2	8·7	19·55

Pool 14. 18 July 1937. High water 5.07 p.m.

Time	Air temp. ° C.	Water temp. ° C. Surface	Bottom	Oxygen % sat.	pH	Chloride g./l.
*7.30 a.m.	17·75	15·5	15·2	57·6	8·3	—
8.0 a.m.	17·75	15·5	15·1	—	8·3–8·4	19·45
8.25 a.m.	18·0	15·5	15·2	68·4	8·3–8·4	—
8.45 a.m.	18·5	15·6	15·2	—	8·4–8·5	—
10.30 a.m.	22·0	16·6	15·2	160·0	8·5–8·6	—
11.0 a.m.	22·25	16·8	15·2	—	8·5–8·6	19·45
11.30 a.m.	22·0	16·9	15·5	169·3	8·6–8·7	—
12.0 noon	22·25	17·3	15·5	—	8·6–8·7	—
12.25 p.m.	23·0	17·6	15·6	198·2	8·6–8·7	—
12.45 p.m.	23·0	18·0	15·5	—	8·6–8·7	19·45
2.30 p.m.	25·25	19·5	15·6	254·6	9·3	—
3.0 p.m.	26·0	20·2	15·8	—	9·3	19·56
3.30 p.m.	24·5	20·2	16·1	271·4	9·3	—
4.0 p.m.	25·0	20·8	15·9	—	9·3	—
*4.25 p.m.	23·5	20·5	16·8	262·7	9·3	19·56
*4.45 p.m.	22·75	20·1	16·1	—	9·3	—
*6.30 p.m.	20·25	16·8	16·3	163·8	9·0	—
*7.0 p.m.	24·25	15·5	15·5	—	8·5	19·51
*7.30 p.m.	24·5	14·7	14·7	107·8	8·5	—
*8.0 p.m.	22·0	14·7	14·7	—	8·5	—
*8.25 p.m.	21·75	14·7	14·7	101·0	8·5	—
*8.45 p.m.	20·0	14·7	14·7	—	8·5	19·36
10.5 p.m.	17·0	14·7	14·7	98·6	8·5	19·36

* Indicates contact with sea.

(*b*) *Daily readings*

July 1937 (chloride content)

Date	Time	Chloride content (g./l.) Pool 3	Pool 6	Pool 7	Pool 10
4th	a.m.	—	19·37	7·17	17·91
	p.m.	15·84	19·27	7·31	18·30
5th	a.m.	15·51	19·29	7·29	19·0
	p.m.	14·31	19·42	—	19·77
6th	a.m.	17·54	19·35	6·55	19·68
	p.m.	18·71	19·3	6·55	19·75
7th	a.m.	19·03	—	6·55	19·92
	p.m.	19·17	19·35	6·65	20·07
8th	a.m.	—	19·38	6·71	19·77
	p.m.	19·06	19·45	6·82	—
9th	a.m.	5·64	18·48	6·44	18·05
	p.m.	16·47	19·38	5·82	19·45
10th	a.m.	10·69	18·31	5·08	15·36
	p.m.	17·69	19·45	5·08	18·43

April 1938 (chloride content)

Date	Time	Chloride content (g./l.) Pool 3	Pool 6	Pool 7	Pool 10
13th	p.m.	19·37	19·37	17·73	20·81
14th	a.m.	18·82	19·34	17·73	19·67
	p.m.	18·77	19·08	17·66	19·50
15th	a.m.	18·35	—	17·8	19·39
	p.m.	18·54	19·24	18·08	19·41
16th	a.m.	18·19	18·98	18·24	19·23
	p.m.	18·27	19·05	18·72	19·13
17th	a.m.	18·67	19·21	18·85	19·49
	p.m.	18·67	19·42	19·38	19·63
18th	a.m.	18·64	19·24	19·56	19·81
	p.m.	18·87	19·58	20·22	20·08
19th	a.m.	18·75	19·54	20·4	20·82
	p.m.	18·52	19·29	20·63	19·95

July 1938 (chloride content)

		Chloride content (g./l.)				
		Pool 3		Pool 6	Pool 10	
Date	Time	Surface	Bottom		Surface	Bottom
14th	a.m.	9·73	13·92	19·17	12·26	14·34
	p.m.	7·88	17·11	19·26	12·43	19·36
15th	a.m.	9·17	17·52	19·35	17·70	18·3
	p.m.	11·57	17·12	19·36	18·33	18·18
16th	a.m.	12·92	17·09	19·26	18·35	18·46
	p.m.	12·41	—	—	18·59	18·49
17th	a.m.	13·39	16·84	19·31	18·49	18·45
	p.m.	13·92	16·41	19·12	18·49	18·49
18th	a.m.	14·32	16·65	18·98	18·69	18·67
	p.m.	14·50	16·58	19·36	18·80	18·85
19th	a.m.	14·41	16·49	19·15	18·86	18·95
	p.m.	14·41	16·47	19·26	18·95	18·77
20th	a.m.	14·73	15·96	18·28	18·84	18·82
	p.m.	14·64	16·1	19·09	18·73	18·8

July 1938 (temperature, oxygen content and *p*H)

Pool 3

Date	Time	Temp. °C. Air	Surface	Bottom	Oxygen % sat.	*p*H
14th	a.m.	18·0	18·8	19·4	141·3	8·8
	p.m.	22·5	23·0	21·9	154·1	9·4
15th	a.m.	17·0	21·3	21·3	136·9	9·3–9·4
	p.m.	23·75	—	23·6	160·1	9·5
16th	a.m.	14·25	21·6	21·9	135·2	8·8
	p.m.	22·25	26·1	24·7	167·1	9·6
17th	a.m.	17·0	22·5	23·0	122·1	9·4–9·5
	p.m.	16·0	22·0	22·9	135·8	9·6
18th	a.m.	20·5	20·2	20·8	94·0	9·6
	p.m.	28·0	25·6	23·8	172·4	9·6+
19th	a.m.	16·5	21·2	22·0	114·3	9·6
	p.m.	16·5	22·3	22·9	144·7	9·6
20th	a.m.	16·0	19·1	20·1	95·3	9·3–9·4
	p.m.	20·0	22·3	21·5	152·6	9·6+

Pool 6

Date	Time	Temp. °C. Air	Water	Oxygen % sat.	*p*H
14th	a.m.	19·75	13·3	108·7	8·5
	p.m.	21·75	19·1	182·1	8·8
15th	a.m.	17·25	13·6	117·9	8·5
	p.m.	26·0	20·0	154·5	8·9
16th	a.m.	15·25	13·1	107·5	8·5
	p.m.	24·25	19·8	165·2	8·7
17th	a.m.	20·5	15·4	110·1	8·5
	p.m.	17·0	16·6	146·6	8·8–8·9
18th	a.m.	19·0	15·5	92·6	8·5–8·6
	p.m.	30·25	21·1	194·3	8·9
19th	a.m.	17·5	15·0	105·4	8·5
	p.m.	19·25	17·9	158·8	8·8
20th	a.m.	16·5	14·4	95·0	8·5
	p.m.	22·0	18·0	192·4	8·8–8·9

Pool 10

Date	Time	Temp. °C. Air	Surface	Bottom	Oxygen % sat.	*p*H
14th	a.m.	16·25	16·6	17·5	105·5	8·7
	p.m.	15·0	21·1	20·0	129·9	9·0–9·1
15th	a.m.	20·0	19·3	17·7	127·5	8·8
	p.m.	16·0	20·8	20·2	150·5	9·1–9·2
16th	a.m.	15·0	15·5	15·5	97·8	8·7
	p.m.	21·25	21·3	20·0	164·5	9·2–9·3
17th	a.m.	22·0	—	17·7	115·4	9·1
	p.m.	16·0	17·5	17·7	120·5	9·3
18th	a.m.	24·0	17·7	16·9	94·3	9·2–9·3
	p.m.	19·0	22·1	20·1	143·0	9·3–9·4
19th	a.m.	17·5	16·9	17·5	87·1	9·1–9·2
	p.m.	16·0	18·3	18·7	133·0	9·5
20th	a.m.	17·0	—	15·9	80·7	9·3
	p.m.	18·5	18·8	18·0	137·4	9·4–9·5

VARIATIONS IN THE GROUND PLAN OF A NEST OF THE ANT, *TAPINOMA NIGERRIMA*

By W. PICKLES

(With 25 Figures in the Text)

1. INTRODUCTION

A nest of the ant *Tapinoma nigerrima* Nyl. was observed from 17 February 1943 to 20 May 1943 at regular intervals of time, roughly every other day, with a few exceptions when pressure of duties prevented observations being made. The nest was situated on one of the foothills in eastern Algeria and was on an uncultivated part of the hillside. These ants build mounds of soil which are not permanent mounds as are those of the ant *Lasius flavus* F., and which are built to be used as nurseries. The survey described below is a record of the building activities of *Tapinoma nigerrima* Nyl. during the early part of 1943 until the mounds were destroyed by some external agent, probably goats, or Arabs, in May, and no further building or repairs were carried out.

Lubbock (1888) describes the building of a nest of *Lasius niger*; and the writer has made observations on the mound-building activities of *L. niger* and *L. flavus* (Pickles, 1943). Like these two species, *Tapinoma nigerrima* builds after rain or during rain if falling lightly, and appears to depend on the mound particles adhering together by moisture and the sun baking hard the newly built structure. The stems of vegetation are used as 'scaffolding' (cf. *Lasius niger* as described by Forel, 1928).

This particular nest was interesting from the very beginning, because unlike many other mounds in the vicinity which were single, several mounds were built clustered together. There was free intercommunication between each mound.

2. DIARY OF BUILDING OPERATIONS

15 *February*. When the area of ground where ants' nests had been located was visited, at the place where the following nest was built, there was no evidence on the surface that an ant's nest existed there.

17 *February*. Five small newly built mounds (A–F) were observed and further building was in progress. Ants were crawling from one mound to another. They were using living grass stems and blades at nest A as scaffolding (cf. Pickles, 1943). The mounds were roughly circular in plan and varied from 3 to 5 in. in diameter (Fig. 1).

19 *February*. A further subsidiary mound had been built (G). This was 7 in. from A and 5 in. from B (Fig. 2).

21 *February*. On the previous day there had been a shower of rain and building had been in progress to such a degree that the mounds B and G had joined together (Fig. 3).

22 *February*. During the afternoon there were several rain showers. By 6 p.m. when the nest was visited, there had been considerable building and the mounds A, B, and G had coalesced, so that there were again five mounds. From now onwards this united mound was designated ABG. This mound was approximately oval in shape, its greatest width being 9 in.

From mound ABG and pointing towards C there was the beginning of a covered passage, extending for a distance of 2 in. Similarly from mound C there was the beginning of a covered passage pointing towards mound ABG and 2½ in. long. Both these passages were 2 in. wide (Fig. 4).

24 *February*. Building had continued apace and with the exception of mound F all the mounds had increased in size. A passage had been built from ABG to C; this was open on top and the total width was 2 in., the walls on an average being ¼ in. in height and the trackway along the centre of ½ in. average width. The walls themselves were on the average ¾ in. wide (Fig. 5).

27 *February*, 3 *p.m.* The walled passage which the ants had built between the mounds ABG and C had been destroyed. Circumstances seemed to suggest the possibility that the ants themselves had destroyed it, because although there had been showers of rain in the morning, none were of sufficient violence to destroy this structure. Mounds E and F were quite small, being 6 and 4 in. in diameter respectively. Mound ABG was now joined to mound D by a covered passage 2 in. in width. This passage and the one previously built between ABG and C was constructed above the general level of the ground and not by tunnelling.

27 *February*, 3.45 *p.m.* At this hour a heavy thunderstorm came on with hailstones up to ¼ in. diameter. The gullies round about were raging torrents for a little while after the storm abated.

27 *February*, 6.30 *p.m.* When the nest was revisited at 6.30 p.m. all the newly built soil of the last few days had been washed away and the mounds were 'rounded off'. The passage between ABG and D was completely washed away and only one ant was observed to be abroad and this was crawling

Fig. 1.

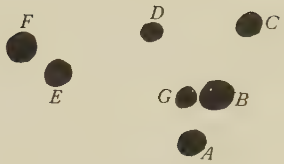

Fig. 2.

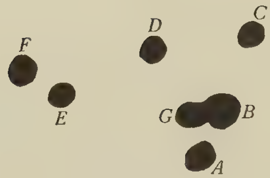

Fig. 3.

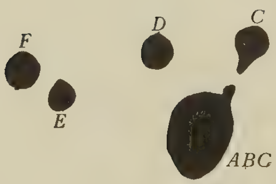

Fig. 4.

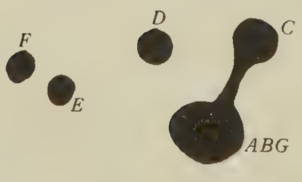

Fig. 5.

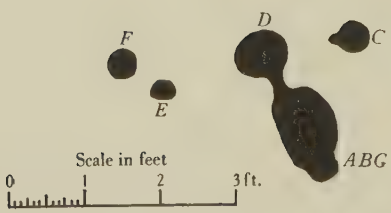

Fig. 6.

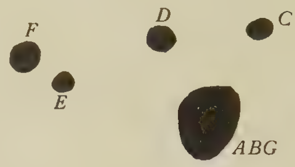

Fig. 7.

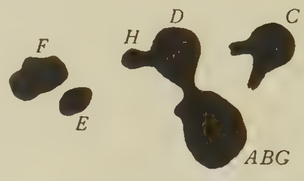

Fig. 8.

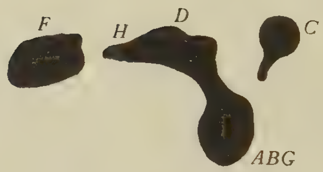

Fig. 9.

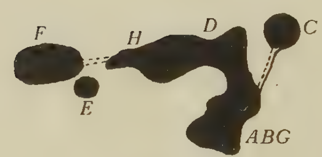

Fig. 10.

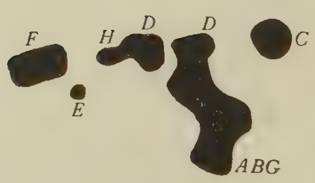

Fig. 11.

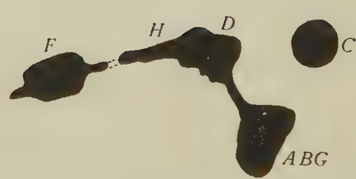

Fig. 12.

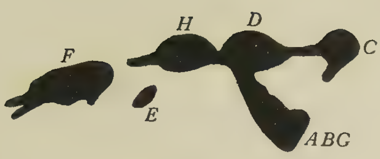

Fig. 13.

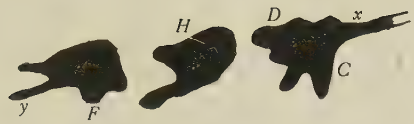

Fig. 19.

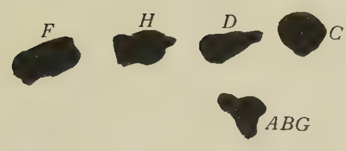

Fig. 14.

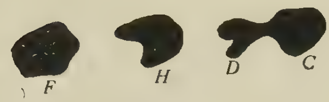

Fig. 20.

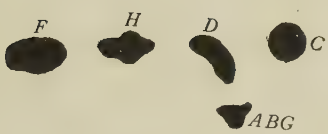

Fig. 15.

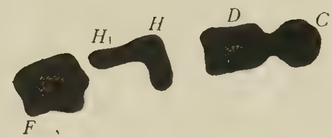

Fig. 21.

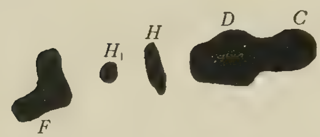

Fig. 22.

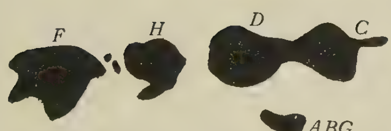

Fig. 16.

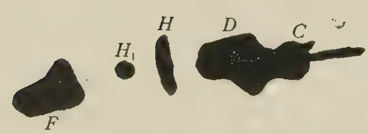

Fig. 23.

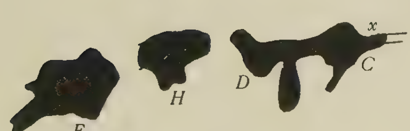

Fig. 17.

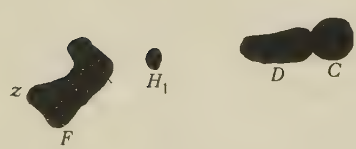

Fig. 24.

Fig. 18.

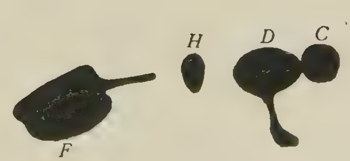

Fig. 25

from nest C towards ABG along the ground previously occupied by the corridors and passages. The entrances to the mounds were plain to see (Fig. 6, before the storm; Fig. 7, after the storm).

28 *February*. Since the previous day there had been considerable building; a new mound had been thrown up, H, oval in shape and measuring 4 × 2 in. This had already been joined to mound D. ABG and D were again joined by a covered passage. From mound C and for a distance of 3½ in. a corridor was in process of construction towards ABG. Also from mound C and for a distance of 3 in. a corridor had been built towards mound D; both these were 2 in. wide. Mound F had been increased in size and was roughly rectangular and measured 9 × 6 in. Mound E was roughly oval in shape and measured 5 × 4 in. (Fig. 8).

7 *March*. During the previous afternoon there was a severe thunderstorm with hail which had done considerable damage to the mounds and destroyed the corridors which were being built from ABG to C and from C to D. However, the ants were busy at the time of observation, rebuilding a passage between C and ABG: this was the third attempt to build a passage between these two mounds. They were also commencing a walled corridor from mound H toward F. Mound F was still rectangular in shape and had increased in size to 11 × 8 in. Mound E was completely washed away and there were no signs of its presence. Mounds ABG, D, and H were now joined together into one mound. The net result was that there were now three mounds, the large one being somewhat triangular in shape and measuring 1 ft. 6 in. × 1 ft. 5 in. and 2 ft. along the 'hypotenuse' (Fig. 9).

9 *March*. The mounds were of much the same plan as on the 7th, except that mound E had made its appearance again and was 3 in. in diameter and roughly circular. From ABG to C one side of a corridor had been completed, but on the other side only a few scattered grains of soil marked the alinement. A covered passage from H to F was completed for a distance of 4 in. from H and was 2½ in. wide at its widest part. From this point to F a corridor was in process of being built; there were walls but no roof (Fig. 10).

11 *March*, 2.45 *p.m.* There was a heavy thunder-shower with hail. 6 *p.m.* The nest was visited so as to observe the effects of the storm. The mounds had been smoothed out and rebuilding had commenced. Mound E was very small, being 2 in. in diameter, and mound F was reduced to a rectangle 9 × 5 in. Mound D had been split in two and the corridors between ABG and C and between H and F were completely destroyed (Fig. 11).

13 *March*. Since the storm of the 11th there had been considerable rebuilding. At D the division of the nest had been repaired and there was no evidence of any further rebuilding at ABG nor any attempts to rebuild the corridor between ABF and C. At mound F there were the beginnings of a covered way beneath a twig in a direction somewhat towards the south-west; the twig gave support to the roof. This was completed for a distance of 2½ in. This was similar to phenomena observed on *Lasius niger* at Woolwich (Pickles, 1943). Between mounds F and H there was a corridor which was covered for a distance of 4 in. from H; the rest of the way the alinement was marked by isolated grains of soil (Fig. 12).

17 *March*. During the night of the 14th there was considerable rain, and when this nest was visited at 2.45 p.m., there had been considerable rebuilding and all the mounds except ABG had been enlarged. A completely covered passage joined mounds C and D and a covered passage had been constructed from mound H towards F for a distance of 4½ in. Mound F had been enlarged to a rectangle, 1 ft. 4 in. × 7 in., and the passage under the twig was still intact. For a distance of 2¾ in. from mound C a passage had been constructed towards ABG.

On this date and at this time the union of all the mounds was nearest completion, there being only three large mounds: (1) ABG, C, D, and H; (2) F; and (3) E (Fig. 13). This state of affairs was soon to be destroyed, for at 5.30 p.m. a heavy thunderstorm broke and destroyed all the mounds. Unfortunately, I was unable to visit the nest after the storm.

19 *March*. The day was showery with many sunny periods, and there was active rebuilding by the ants. There had been considerable building since the storm of the 17th, but all the passages were destroyed. All the mounds were smaller than they were on that day, and the state of affairs at 2.15 p.m. is shown in Fig. 14. Between that time and 3 p.m. there was a heavy storm when, although the shapes of the mounds were roughly the same, they were all of smaller dimensions (Figs. 14, 15).

21 *March*. Since the rain of the 19th there had been considerable building and all the mounds were increased in size, C and D being joined together. From mound H a passage had been built for a distance of 4½ in., and from C there was also a covered way extending for 4 in. and being 1 in. wide. Mound ABG was quite small (Fig. 16).

23 *March*. The day was fine and sunny and there was great building activity. All the mounds were larger than when last observed. ABG was joined by a passage 3 in. wide to D and D was joined to C also by a covered way 3 in. wide. From mound C there were covered passages to ABG for a distance of 3½ in., and in an opposite direction to the long axis of the nest there was a covered way (x) constructed for a distance of 5 in., the side walls of which, without roof, were continued for a further distance of 3 in. (Fig. 17).

25 *March*. Further building had been done since the 23rd and all the mounds had increased in size. The passage between ABG and D was absent and C and D were still joined together. There were three

covered passages leaving mound C; two of these were 4 in. long, and passage x referred to above was still covered for a distance of 5 in. and the walls alone continued for a further 3 in. (Fig. 18).

27 *March*. There had been very little building, as there had been very little rain for eight days and the ground was hard and dry. The passage x from mound C had been increased to 10 in. in total length, 7 in. of which were covered. Mounds C and D were still joined together and a covered passage from mound F (y) was $5\frac{1}{2}$ in. long and $1\frac{1}{2}$ in. wide at its widest part (Fig. 19).

29 *March*. During the previous afternoon and the morning of this day there was considerable rain and the mounds had been smoothed out; all passages having been washed away. Rebuilding was in progress when the nest was visited at 2.15 p.m. The mounds were smaller in size than on the 27th and there was building at mound F. From this time onwards mound E did not show itself again as a separate mound. Mounds C and D were still joined together and remained so for the rest of the time during which observations were made (Fig. 20).

31 *March*. This day was showery with sunny intervals. Mound F was increased in size and the combined mounds C and D were increased in size and also altered in shape from the previous record. Since the 25th there had been no sign of mound ABG (Fig. 21). A nursery was established by these ants under a stone at a distance of 10 ft. from mound C; little building took place there.

4 *April*. After three days when rain fell the nest was revisited at 2.15 p.m. Mound F had been altered in shape to a reversed 'L'. Between mounds F and H there was a small mound H_1, roughly circular in shape with a diameter of 3 in. The combined mounds C and D measured 1 ft. 8 in. long with a maximum width of 9 in. All the mounds were separate, and there was no attempt to construct covered passages from one to the other (Fig. 22).

6 *April*. The mounds were approximately arranged in a straight line and mound H_1 was still present and had not increased in size. Mound H itself was oval in shape and longer but no wider. The combined mound CD was the same length, 10 in. wide at its widest part. From C and running in an easterly direction there was a covered passage $8\frac{1}{2}$ in. long and $1\frac{1}{2}$ in. wide. There was also another passage running east and a little to the north of the one mentioned above (Fig. 23).

23 *April*. Unfortunately, owing to pressure of work, I was unable to visit the nest from 6 until 23 April. The mounds were much smaller than on the 6th, with the exception of mound F which had an extra extension to the north (z). Mound H had disappeared, though H_1 was still present. Mounds C and D were touching each other, with a line of demarcation between them. The mounds were more regular in shape and with fewer protrusions (Fig. 24).

2 *May*. During the afternoon of the previous day there was a heavy thunder shower; to-day when the mounds were visited there had been considerable rebuilding. Mound F was increased in size and was once more rectangular in plan. From it there was a passage running for a distance of 9 in. towards H which was $\frac{3}{4}$ in. wide. From mound D which was again touching mound C there was a passage 10 in. long and $\frac{3}{4}$ in. wide running to the old site of mound ABG. It may be that mound ABG has been renewed again (Fig. 25).

4 *May*. The mounds had been destroyed by some external agent, probably goats or even Arabs, and there had been no attempt by the ants to repair them.

8 *May*. During the previous day there was a heavy rain shower, but when the mounds were visited at 6.30 p.m. there had been no further attempt at repairing them though the ruins were still inhabited.

10 *May*. Though the ants were still inhabiting the ruins of the nests there was still no attempt to repair them. Submound I, the 'nursery', was now deserted.

12 *and* 16 *May*. The mounds were still inhabited, but no repairs had been carried out.

20 *May*. As the rainy season was over and there had been no attempt to repair the damage done to the mounds on 4 May, it was considered unnecessary to carry on these particular investigations any further. The ants appeared to have abandoned the attempt to repair the mounds again.

3. DISCUSSION

The observations made on the ground plan of a nest of *Tapinoma nigerrima* illustrate the fact that even the mounds which this ant builds to use as nurseries in the early part of each year are more temporary than at first appears. They vary from day to day according to the prevailing weather; they are in striking contrast to the mounds of *Lasius flavus*, the ground plans of which are only altered over a period of years. The nest which was the subject of the present survey was particularly interesting because subsidiary nests were built from the beginning. This does not always take place, as several other nests of the same species of ant on the same hillside were composed of one mound only.

4. SUMMARY

1. A diary of the variations of the ground plan of a nest of the ant *Tapinoma nigerrima* in Algeria is described, beginning on 15 February 1943 and ending on 20 May 1943.

2. The survey emphasizes the point that although the mounds are temporary ones they are constantly undergoing a change of ground plan from day to day. This is in striking contrast to the mound of such a species of ant as *Lasius flavus*, which is added to year by year and forms a permanent 'landmark' on the

area. No account was taken of the subterranean extent of the nest.

3. Building operations were strongly dependent on rainfall, light rains making possible the working of the soil, heavy rains destroying part of the built mounds.

5. ACKNOWLEDGEMENTS

I wish to express my gratitude to Mr H. St J. Donisthorpe for kindly identifying the ants for me, and to Mr C. B. Spencer for typing the manuscript.

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THE FAUNA OF THE RIVER TEIFI, WEST WALES

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(With 3 Figures in the Text)

1. INTRODUCTION

In 1919 Carpenter began a series of studies (1924, 1925, 1926) on the fauna of the rivers and streams of west Wales, particularly the Aberystwyth district of Cardiganshire. These investigations were stimulated by the fact that the rivers Rheidol and Ystwyth had been completely devoid of fish for many years, and very lacking generally in fauna and flora. While popular opinion associated this with the mining, washing and crushing of lead, zinc and silver ores which was carried on so extensively in the district during the nineteenth century, no systematic study of the problem had been made. Carpenter's first investigations (1922, 1924) dealt with the rivers Rheidol, Ystwyth and Clarach; it was shown that the lower reaches of the two former rivers supported a very scanty fauna consisting entirely of Arthropoda, apparently the result of pollution by lead salts in solution; that the latter was mainly polluted near the source of its chief head-water, the Nant Silo; and that its fauna underwent a progressive improvement as the stream was joined by more and more unpolluted tributaries on its journey to the sea.

At the present time, many years after the complete cessation of mining operations, the derelict mine-workings continue to have marked effects on the chemical and physical nature of the rivers nearby. The drainage of surface water from vast dumps of mine refuse still carries dissolved lead and zinc salts into the rivers, and though this mode of pollution has become unimportant in the case of the Rheidol and the Ystwyth, the drainage of surface water from the East Daren mine at Cwm Symlog still seems to cause a continual pollution of the Nant Silo, which remains devoid of fish. In the case of the Ystwyth (Jones, 1940*a*) a steady discharge of water containing 20–60 mg./l. of dissolved zinc, which leaves certain adits at the Frongoch and Cwm Ystwyth mines, maintains the river in a state of constant pollution twenty years after the cessation of mining. The Rheidol continues the gradual process of recovery described by Laurie & Jones (1938). The process of silting up of the river beds also continues; this is most marked in the case of the Ystwyth, where long stretches of the river bed present a vast expanse of rubble and gravel, five or six times the width of the actual water channel, which frequently changes its course. The same is true, to a less extent, of the Rheidol; recently the river cut across a meander about two miles from its mouth, forming the usual ox-bow lake. This lake had a very brief existence, and in a few weeks was almost completely filled up by mine-dump refuse deposited by the flooding river.

The study of the way the fauna of these rivers has been selectively limited by these factors has proceeded along three main lines: (1) Faunistic studies of the polluted streams themselves, designed to show which animal groups are unrepresented; (2) experimental work in the laboratory and the field designed to find the approximate concentrations at which the pollutants are fatal to the different animals, and the nature of their toxic effect; and (3) comparison of the fauna of the polluted streams with that of unpolluted waters of the same district.

The extensive silting up of the rivers with vast quantities of mine refuse consisting of material in all states of division from large stones to fine sand gives these rivers a peculiar physical character. How far this peculiar physical nature of the streams in question determines the nature of the fauna they support is a problem which has not received much attention, and as this problem is obviously difficult to elucidate experimentally the most hopeful line of investigation would appear to be the last of those just enumerated. In her early work Carpenter did not carry out any intensive faunistic surveys of the unpolluted streams of the district, and in her general study (1924) of the fauna of polluted Cardiganshire rivers the Capel Dewi Brook or Peithyll was the only unpolluted basis of comparison selected. This choice was a little unfortunate, for the Peithyll is a very small stream, and though unpolluted at that time was really in the process of recovery. In the *Report of the Rivers Pollution Commission appointed in* 1868, written evidence (1874, p. 51) states that up to about 1848 the Peithyll was heavily polluted and devoid of fish, that the washing of ores in its valley then ceased, and that the stream was then successfully restocked with trout. Carpenter (1924) recorded twenty-three animal species for the Peithyll; a faunistic survey of the same stream (unpublished) made in 1937–9 by the writer and Donald R. Arthur indicated a considerably richer fauna comprising at least seventy-eight species, which suggests that at the time of Carpenter's study recovery was by no means complete.

The lack of faunistic study of the unpolluted

waters of the district has been pointed out by the writer (1941) in a paper dealing with the fauna of the river Dovey and designed to provide, in some measure, the required background. The present paper, dealing with the river Teifi, is a further general ecological study to the same end.

2. PREVIOUS STUDY OF THE RIVER

There is little or no evidence to suggest that the fauna of the river has ever been affected to any serious extent by metallic pollution; in the nineteenth century a small number of metalliferous mines were active near its head-waters, the most important of these being the Esgairmwyn mine at which lead, zinc and silver ores were mined. This mine was abandoned in 1846, reopened during the 1914–18 war and closed in 1918. The mine was again opened in 1924, and now the possibility that pollution resulting from its activities would injure the Teifi fishery attracted attention immediately. Carpenter (1926) pointed out that the effluents from the mine were causing a rapid deterioration in the fauna of the Marchnant, the head-water of the Teifi into which they were discharged, and that there was grave danger of eventual injury to the main river. Accordingly, efforts to safeguard the river were made; a few yards below the point at which the effluents from the mine were discharged into the Marchnant the stream was weired and its waters diverted to run along a long leet which eventually reached the river Ystwyth below Pontrhydygroes. The device does not appear to have been particularly successful and the building of a launder was proposed; this would enable the effluent's waters to be carried across the Marchnant and on to the Ystwyth without entering the Teifi head-water at all. This launder was never constructed, but the problem was solved in 1928 by the final cessation of activity at Esgairmwyn.

The river probably receives a certain amount of sewage pollution, but its valley is not thickly inhabited, and as far as the writer is aware there is no evidence to suggest that such pollution is in any degree excessive. Milk factories in the valley constitute a potential danger, but at present adequate plant has been installed to deal with the milk washings they have to dispose of.

3. THE RIVER TEIFI SURVEY

(*a*) *Topography: the regions examined* (Figs. 1–3)

The river has its source in Llyn Teifi, one of a group of six lakes situated at an altitude of 1300–1450 ft. on the southern edge of the Plynlimmon plateau. Four trickles of water leave the lake, merge together and are joined by a fifth stream from the small lake lying to the north-west and the stream, now 4–5 ft. wide, plunges down the valley at a gradient of over 350 ft. per mile. Here (collecting region A) the flow of the water is excessively rapid; no loose stones lie on the stream bed, which is mainly made up of solid rock and large boulders, most of these being firmly embedded in the underlying soil. At the margins of the stream there is a fairly abundant growth of mosses, here and there clumps of grass are submerged, and in this very indifferent shelter a few Trichoptera, Ephemeroptera and Coleoptera seem to maintain what must be a precarious existence.

Two miles from its source the stream is joined by another of equal size which has its source in the most easternly of the group of lakes, Llyn Egnant. Its gradient now slackens abruptly to 40–50 ft. per mile and the river has broadened out to a width of 15–20 ft., the water now flows comparatively gently over a bed composed of loose stones, pebbles and gravel bearing a rich algal vegetation, and at points where the water flows rapidly over large stones the moss *Fontinalis antipyretica* is abundant. In this region a second fauna-sampling station (B) was selected, 2½ miles from the source of the river and near Strata Florida abbey. About 5 miles below station B the river reaches the Tregaron bog, a raised bog some 3 miles in length (north-east to south-west) and 1½ miles in width (see Godwin & Mitchell (1938) and Godwin & Conway (1939) for a description of the bog and its ecology), its gradient now falls to only 1½–2 ft. per mile and the river wanders sluggishly through a vast quagmire. When the river is not in flood the flow of water can scarcely be detected and it virtually consists of a long series of deep stagnant pools connected by short links of relatively shallow water, while towards the south-west end of the bog the river swells out into broad and muddy shallows. Along the river bank in the bog region the vegetation forms a well-defined 'river terrace', the most abundant plants on which are *Juncus effusus*, *Phalaris arundinacea*, *Deschampsia caespitosa*, *Carex acuta*, *Galium palustre*, *Ranunculus acris* and *Equisetum* sp. (Godwin & Conway, 1939, p. 325). The submerged vegetation is abundant; *Nymphaea alba* grows at the sides of the deep pools, and the more shallow parts of the river bear a plentiful growth of *Potamogeton natans*, *Myriophyllum* sp., *Ranunculus aquatilis* and *Callitriche aquatica* with patches of *Glyceria fluitans* at the margins. This is sampling region C, collecting being done at various points from Pont Einon, at the south-west end of the bog to the shallows 1½ miles above.

Below Tregaron the gradient of the river increases again to about 10 ft. per mile and, swollen by numerous tributaries to a width of 70–100 ft., the river flows in a generally south-west direction to Lampeter. This section of the river is characterized by the great abundance of the aquatic vegetation: at many points great beds of *Ranunculus* and *Callitriche* stretch almost from bank to bank. Most of the collecting in this region (D) was done at Pont Gogoyan, about 7 miles above Lampeter; here the river is shallow above the bridge, flowing swiftly

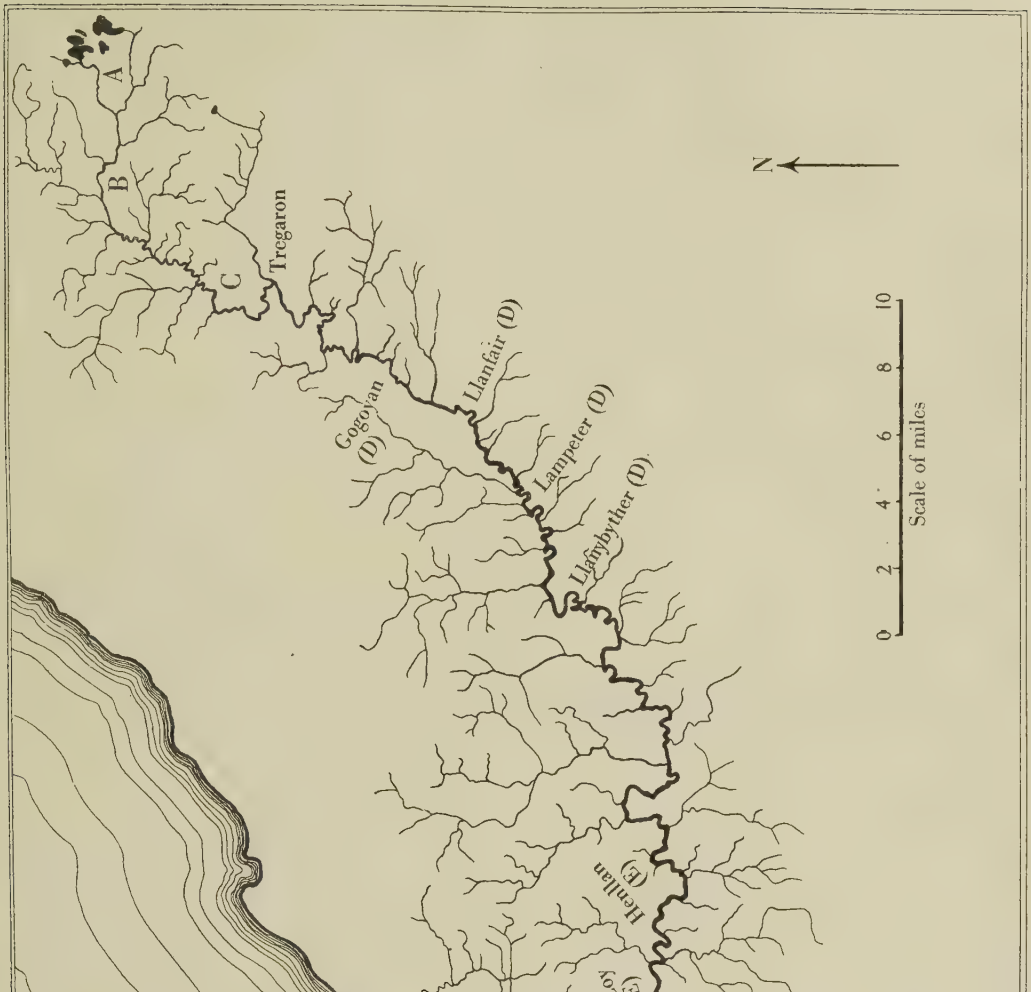

Fig. 1. General map of the river Teifi and its tributaries showing the positions of the regions sampled and other localities named in the text.

over loose stones in midstream and spreading out on its western side into placid shallows where its substratum is composed of sand and mud and there is an abundant growth of *Potamogeton*, *Myriophyllum*, *Callitriche* and *Glyceria*. Collections were also made at Llanfair, 3 miles farther down the river, at Lampeter and at Llanybyther.

Between Lampeter and Llanybyther the aquatic vegetation gradually becomes less and less abundant so that at Llanybyther the river appears almost devoid of plant life. The lower reaches of the river, from Llandyssul to Llechryd constitute region E, and here the river is so varied in character that no single collecting station would be sufficiently representative. Collecting was done at three localities: (1) Henllan bridge. Here the river is 150–200 ft.

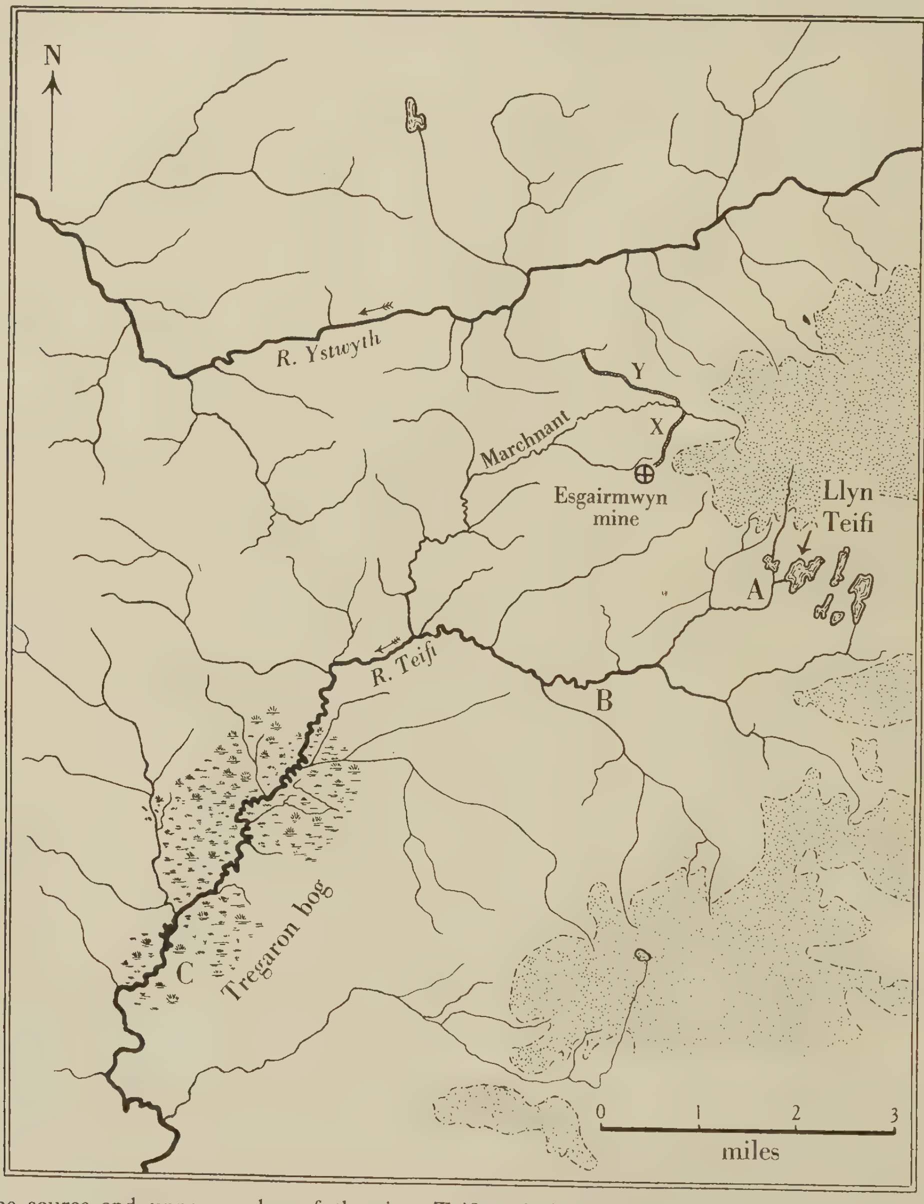

Fig. 2. The source and upper reaches of the river Teifi and the neighbouring region of the river Ystwyth, showing the position of the Esgairmwyn mine, the Tregaron bog and the position of collecting regions A, B and C. *X* is the leet along which the effluent waters from the mine passed into the Marchnant, *Y* is the approximate course of the leet constructed to divert the polluted Marchnant waters into the river Ystwyth. The 1500 ft. contour is drawn and land over 1500 ft. shaded.

wide and heavily shaded by trees, and its bed is rocky and extremely irregular so that at low level the river consists of a great number of rocky pools, some filled with pebbles and sand, through which the water runs at widely varying speeds. Vegetation, particularly *Oedogonium* sp. and *Fontinalis antipyretica*, is abundant. (2) Cwm Coy, where the river is shallow, flowing rapidly over a bed of stones and pebbles covered with heavy deposits of silt, and spreading out at the meanders into deep pools and broad shallows with great accumulations of putrefying mud and flood refuse. (3) Llechryd bridge, where the tidal reaches of the river begin. Here the vegetation has once more become abundant and beds of *Myriophyllum*, *Callitriche* and *Ranunculus* are supplemented by masses of *Elodea canadensis*.

The mainstream, from its source to Llechryd, measures some 75 miles and the mean annual rainfall is 50–60 in. for the upper two-thirds of the river basin and 40–50 in. for the remainder. The river has over seventy tributaries but none of these are of large size, few exceeding 10 miles in length, so that the lower reaches of the river normally carry less water than the Dovey, a river with a much shorter mainstream.

(*b*) *The river water*

The water of the river, like that of other rivers of the district, is soft; an analysis given by Carpenter (1925, p. 13) shows that it has a composition very similar to that of the Rheidol, its total solid matter being 4·4 g. per 100 l. No observations have been made on the oxygen content of the water; in the swift-flowing upper reaches of the river the oxygen content may be safely assumed to be near saturation; in the stagnant pools in the bog region, with dense growth of vegetation, the oxygen content probably undergoes a considerable degree of diurnal and seasonal variation. An intensive study of diurnal and seasonal variation in the oxygen content of the waters of a small lake in the Aberystwyth district, certain parts of which carry a heavy growth of vegetation, has been made by Laurie (1942*a*, *b*). Unfortunately facilities did not permit of similar study on the river.

The Teifi water tends to be slightly less acid than that of the other rivers of the district. Typical *p*H figures for the different regions are: region A, 6·8; B, 6·8; C, 6·6; D, 6·8; and E, 6·8–7·0.

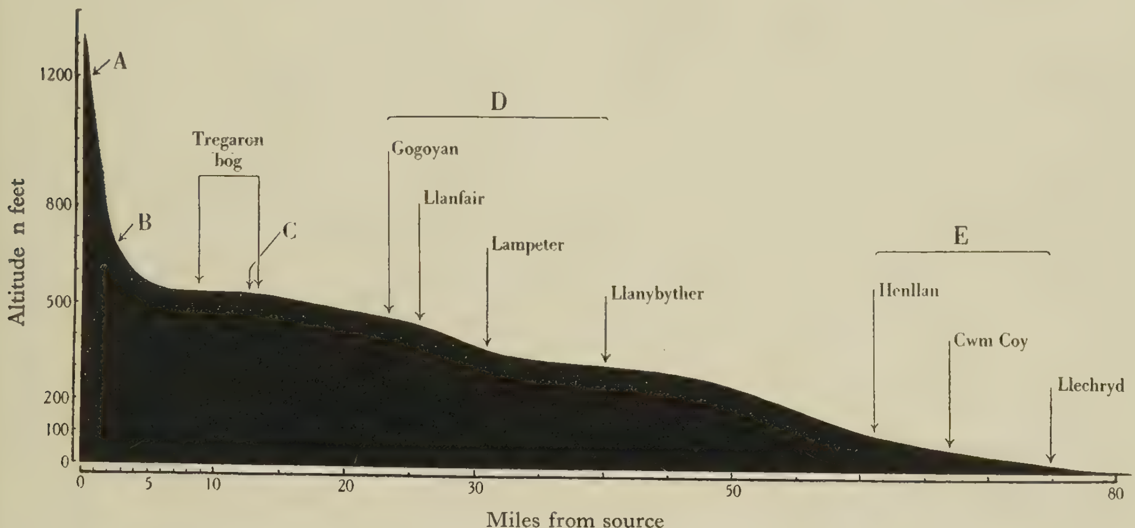

Fig. 3. Elevation of the mainstream of the river Teifi showing the positions and altitudes of the regions examined. The distances include all the river's windings.

(*c*) *Method of sampling the fauna, and sampling dates*

As in previous studies of the same type no attempt was made to sample the fauna quantitatively. The river is so large and varies so greatly in character from place to place that it is very doubtful whether quantitative methods of sampling would yield any valuable result unless carried on on a very large scale. The collecting methods followed very closely those described in the writer's account of the fauna of the river Dovey (Jones, 1941, p. 16), the trawl net being found very useful in region C, at Cwm Coy and Llechryd. Each fauna sample involved about an hour's collecting.

It proved to be quite hopeless to sample at regular time intervals; the river is subject to heavy floods of long duration which make satisfactory collecting

impossible. The actual sampling dates and the localities sampled were as follows:

Region	Date	Locality
A	12 Oct. 1940	½ mile from Llyn Teifi
	26 Apr. 1941	½ mile ,,
	4 Nov. 1942	½ mile ,,
B	30 Sept. 1940	Near Strata Florida Abbey
	15 Feb. 1941	,, ,,
	16 Mar. 1941	,, ,,
	20 Apr. 1941	,, ,,
	18 May 1941	,, ,,
	10 June 1941	,, ,,
	10 Feb. 1942	,, ,,
	12 Sept. 1942	,, ,,
C	20 Sept. 1940	Pont Einon region of Tregaron bog
	1 Oct. 1940	,, ,,
	1 Dec. 1940	,, ,,
	2 Mar. 1941	,, ,,
	19 Apr. 1941	,, ,,
	6 May 1941	,, ,,
	30 May 1941	,, ,,
	18 May 1942	,, ,,
D	5 Oct. 1941	Llanfair
	8 Nov. 1941	Pont Gogoyan
	13 Dec. 1941	,,
	14 Mar. 1942	,,
	18 May 1942	,,
	26 July 1942	,,
	8 Sept. 1942	Lampeter
	8 Sept. 1942	Llanybyther
E	11 Oct. 1941	Cwm Coy
	4 Nov. 1941	,,
	17 Jan. 1942	Henllan
	4 Mar. 1942	,,
	14 May 1942	,,
	16 July 1942	Llechryd

(*d*) *The fauna*

The animals found are listed in Table 1, which gives the numbers taken in the different regions' samples or their degree of abundance. As in previous studies by the writer, attention has been concentrated on the macrofauna and no attempt was made to collect and identify Protozoa, Nematoda and Rotifera. Specimens of all the species recorded, except very familiar animals, have been preserved at the Zoology Department at Aberystwyth. The literature used for the identification of the animals included all the works cited in the second section of the reference list appended to the writer's paper on the river Melindwr (Jones, 1940*b*), and in addition the monographs on *The British Hydracarina* by Soar & Williamson (1925–9), that on the *British Water Beetles* by Balfour-Browne (1940), that on *British Fresh-water Copepoda* by Gurney (1931–3), and Macan's key to the British species of Corixidae (1939).

The minnow is the most abundant fish, particularly in the middle reaches of the river. The river provides excellent fishing for trout, sea trout and salmon, though much damage is undoubtedly done by poachers, particularly in the Tregaron bog district where their activities are not readily detected. Otherwise the vertebrate fauna is very limited, for no coarse fish are caught and there is a somewhat puzzling absence of Amphibia.

The whole fauna list includes about 147 species, the lower reaches of the river displaying the most varied fauna, 84 species being recorded in region E, 81 in D, 68 in C, 58 in B and 28 in A. In region E 13 species are recorded as numerous or very numerous, against 9 at D, 11 at C, 8 at B and none at A. Region A on account of its inaccessibility was visited on three occasions only, and it is possible that more frequent collecting might have lengthened the fauna list for this station to some extent. In region B the fauna is predominantly lotic and resembles that of the upper course of the river Dovey, though slightly richer in Hydracarina and Ephemeroptera. In the bog region the fauna is predominantly lentic, the dominant animals here are Hydracarina, *Cyclops*, *Centroptilum*, *Sigara*, *Anabolia*, Chironomidae and the minnow, but the development of a very rich lentic fauna in this region is probably prevented by the violent flooding that occurs periodically and which must tend to sweep away small animals that can neither swim against the current nor seek refuge in vegetation or bottom deposits.

The fauna of region D resembles that of region C, with the addition of some Plecoptera and campodeiform Trichoptera. That of region E resembles that of the lower reaches of the Dovey but is much less rich in Hydracarina and Coleoptera.

The writer (1941, p. 22) has compared the fauna of the river Ystwyth with that of the river Dovey and has shown that the poverty of fauna of the former appears to be only partly due to the toxic action of the dissolved zinc salts with which its waters are polluted, and that the vastly greater richness of the fauna of the Dovey rests on the presence of a large number of lentic species whose existence in the Ystwyth is made impossible, not by the chemical nature of its waters but by the unfavourable physical nature of the river. The Ystwyth is excessively silted up with constantly shifting accumulations of broken rock, rubble and gritty sand and gravel, almost everywhere shallow and swift-flowing, and practically devoid of vegetation. This lack of vegetation has not been completely explained: it may be partly due to direct toxic action by the polluting metals, but it is probably associated also with the lack of stability of the river bed. The latter explanation is supported somewhat by the fact that miles of the lower reaches of the river Rheidol remain almost entirely devoid of macroflora, despite the fact that here pollution by lead and zinc salts has remained at insignificant levels for over 10 years, and the absence of macroflora in this river appears to be almost certainly associated with the instability of the river bed; at Penybont, near Aberystwyth, where

Table 1. *The fauna of the mainstream of the river Teifi*

The figures give the number of specimens captured in the different regions of the river. When the number of specimens captured was between 100 and 500 the symbol N (numerous) is inserted; when the number exceeded 500 the symbol VN (very numerous) is used. F and C signify 'few' and 'common', respectively, in cases where more precise data cannot be given.

Region ...	A	B	C	D	E
PORIFERA					
Ephydatia fluviatilis (L.)	.	C	.	C	.
PLATYHELMIA					
Polycelis nigra Müll.	.	.	3	6	7
P. cornuta (Johnson)	.	.	.	.	50
OLIGOCHAETA					
Eiseniella sp.	.	.	.	4	.
Lumbriculus variegatus Müll.	.	4	23	18	N
Other spp.	.	.	.	N	VN
HIRUDINEA					
Helobdella stagnalis L.	.	.	2	.	.
Herpobdella atomaria Carena	1	24	4	26	19
Protoclepsis tesselata Müll.	.	.	3	.	.
Glossosiphonia complanata L.	.	.	1	3	2
CRUSTACEA					
Cyclops spp. (mainly C. albidus Jurine)	.	.	VN	F	F
Ostracoda spp.	.	.	6	.	.
Eurycercus lamellatus Müll.	.	.	6	.	2
Asellus aquaticus L.	.	.	31	34	N
Gammarus sp.	.	.	.	.	N
MOLLUSCA					
Sphaerium sp.	.	.	N	4	.
Pisidium sp.	.	.	.	.	VN
Ancylastrum fluviatile (Müll.)	.	31	.	.	2
Limnaea pereger (Müll.)	.	.	.	3	N
Hydrobia sp.	.	.	.	.	N
Planorbis spirorbis (L.)	.	.	.	4	.
HYDRACARINA					
Pseudosperchon verrucosus (Protz.)	.	23	.	.	.
Sperchon spp.	.	21	.	.	.
Diplodontus despiciens (Müll.)	.	2	.	2	1
Teutonia primaria Koen.	.	.	6	N	.
Limnesia fulgida C. L. Koch	.	.	3	.	.
L. maculata (Müll.)	.	.	19	4	.
L. koenikei Piers.	.	.	67	4	.
Lebertia celtica Sig Thor	.	13	.	.	.
L. porosa Sig Thor	7	8	39	N	N
Oxus strigatus (Müll.)	.	.	4	.	.
Atractides spp.	.	13	.	.	1
Hygrobates longipalpis (Herm.)	.	21	VN	1	4
Unionicola crassipes (Müll.)	.	.	N	1	4
Piona sp.	.	.	.	.	1
Wettina podagrica C. L. Koch	.	.	12	.	.
Aturus scaber (Herm.)	.	15	.	.	.
Brachypoda versicolor (Müll.)	.	.	6	2	.
Momonia falcipalpis Halb.	.	.	1	.	.
Mideopsis orbicularis (Müll.)	.	.	5	12	.
Arrhenurus maculator (Müll.)	.	.	.	.	1
A. ornatus George	.	.	1	.	.
Arrhenurus sp. *a*	.	.	.	.	1

Region ...	A	B	C	D	E
COLLEMBOLA					
Isotomurus palustris (Müll.)	.	7	.	1	.
PLECOPTERA					
Perlodes sp.	2	19	.	.	5
Perla sp.	.	3	.	5	.
Isoperla sp.	45	56	.	26	14
Isopteryx sp.	28	N	.	25	1
Nephelopteryx nebulosa L.	.	.	.	7	8
Taeniopteryx sp.	.	29	.	2	.
Leuctra sp. *a*	6	N	.	1	5
Leuctra sp. *b*	.	.	.	.	15
Nemoura sp. *a*	.	N	.	.	3
Nemoura sp. *b*	21	N	.	4	2
Nemoura sp. *c*	2	.	.	2	2
EPHEMEROPTERA					
Ephemera sp.	.	.	.	.	1
Rithrogena semicolorata Curtis	.	26	.	.	4
Ecdyonurus sp.	.	57	.	12	5
Leptophlebia sp.	27	.	23	.	.
Ephemerella sp.	.	2	.	N	1
Coënis sp.	.	8	6	30	N
Centroptilum sp.	.	.	N	4	.
Baëtis sp.	20	VN	27	N	N
Siphlonurus sp.	.	.	3	.	.
Chloëon sp.	.	.	2	.	.
ODONATA					
Cordulegaster boltoni Donov.	.	.	.	.	1
Calopteryx sp.	.	.	27	18	6
Pyrrhosoma nymphula Sulz.	.	.	9	5	.
Ischnura elegans Van der Lind.	.	.	14	5	.
HEMIPTERA					
Hydrometra stagnorum L.	.	.	.	3	.
Velia currens Fab.	1	2	.	23	1
Gerris najas De G.	.	12	.	.	.
G. costae H. Schff.	.	6	.	.	.
G. lacustris L.	.	.	3	4	2
Gerris spp. nymphs	.	.	.	41	.
Nepa cinerea L.	.	.	1	.	1
Plea minutissima Fab.	.	.	.	.	2
Aphelocheirus aestivalis Fab.	.	.	.	2	2
Sigara striata Fieb.	.	.	VN	N	3
S. semistriata Fieb.	.	.	.	.	14
S. fallenii Fieb.	.	.	N	.	4
Micronecta poweri (D. & S.)	.	.	.	.	11
Corixidae spp. nymphs	.	.	N	N	VN
NEUROPTERA					
Sialis sp.	.	.	30	2	1
TRICHOPTERA					
Phryganea sp.	.	.	1	.	.
Limnophilus marmoratus Curt.	.	.	42	.	.
Limnophilus sp. *a*	.	.	19	.	.
Anabolia nervosa Curt.	.	.	VN	VN	.
Stenophylax stellatus Curt.	.	3	.	1	4
Halesus radiatus Curt.	20	5	38	8	14
Sericostoma personatum Spence	.	14	.	14	10
Goera pilosa F.	.	.	5	.	.
Silo pallipes F.	1	2	.	.	.
Brachycentrus subnubilis Curt.	.	.	.	8	7
Lepidostoma hirtum F.	.	7	1	.	37
Beraeodes minuta L.	.	.	10	.	.

Table 1 (*continued*)

Region ...	A	B	C	D	E
TRICHOPTERA (*cont.*)					
Leptocerus sp.	.	.	3	4	6
Mystacides sp.	.	.	4	22	30
Triaenodes sp.	.	.	2	7	.
Hydropsyche pellucidula Curt.	6	28	.	1	8
H. instabilis Curt.	1	15	.	20	34
Polycentropus flavomaculatus Pict.	7	8	.	3	3
Plectrocnemia conspersa Curt.	9	6	.	.	.
Philopotamus montanus Donov.	.	.	.	27	.
Rhyacophila dorsalis Curt.	.	38	.	1	.
Rhyacophila sp. *a*	.	.	.	.	1
Glossosoma boltoni Curt.	.	.	.	.	3
Hydroptila sp.	.	.	.	2	.
Ithyetrichia lamellaris Eaton	.	.	.	1	.
Oxyethira sp.	.	1	.	7	.
COLEOPTERA (imagines)					
Gyrinus natator L.	.	.	.	.	1
G. urinator Ill.	.	.	.	.	1
Haliplus fulvus Fab.	.	.	16	.	.
H. lineatocollis Marsh	.	.	.	4	3
H. flavicollis Sturm.	.	.	3	.	.
H. ruficollis De G.	.	1	12	.	.
H. fluviatilis Aubé	.	.	4	.	.
Deronectes elegans Pz.	.	.	3	8	28
Graptodytes pictus F.	1	1	12	.	.
Hydroporus discretus Fair.	.	1	.	.	.
Oreodytes rivalis Gyll.	1	13	1	2	5
O. septentrionalis Gyll.	.	.	.	.	8
Platambus maculatus L.	.	.	9	8	.
Helophorus aquaticus L.	.	.	.	.	1
H. affinis Marsh	.	.	4	2	.
H. brevipalpis Bed.	.	.	.	2	3

Region ...	A	B	C	D	E
Anacaena globulus Pk.	.	1	.	.	.
Hydraena gracilis Germ.	1	32	3	3	.
Limnebius truncatellus Thunb.	.	3	.	.	6
Latelmis volkmari Pz.	1	15	.	.	2
Limnius tuberculatus Müll.	3	12	2	3	14
Esolus parallelopipedus Müll.	.	8	.	3	7
COLEOPTERA (larvae)					
Dytiscidae	.	3	18	.	.
Gyrinidae	.	3	.	.	2
Haliplidae	.	.	3	.	.
Helmidae	.	8	.	15	3
Helodidae	.	2	.	.	.
DIPTERA					
Tipula sp.	.	.	.	2	2
Dicranota sp.	1	8	.	8	.
Chironomidae spp.	.	N	N	32	9
Dixa spp.	.	4	1	.	.
Forcipomyia sp.	.	4	.	14	.
Anopheles maculipennis Meig.	.	.	.	1	8
Simulium spp.	42	N	5	.	1
Tabanus sp.	1	2	1	5	11
Leptididae sp.	.	.	.	7	1
VERTEBRATA					
Petromyzon marinus L. (sea lamprey)	.	.	.	.	2
Phoxinus phoxinus (L.) (minnow)	.	C	VN	VN	VN
Gasterosteus aculeatus L. (stickleback)	.	.	.	4	N
Salmo trutta L. (trout)	See text				
S. trutta L. (sea-trout)	See text				
S. salar (salmon)	See text				

high banks confine the river to a constant course, a fair amount of phanerogamic vegetation survives.

This general conclusion regarding the fauna of the Ystwyth is supported by the present investigation; the long fauna list for the Teifi includes about 94 species not recorded for the polluted river, and of these 24 at most belong to animal groups recognized as being sensitive to metallic pollution.

It is not possible to make a complete comparison between the fauna of the Rheidol and that of the Teifi, for only the lower reaches of the Rheidol have been surveyed. This part of the river was surveyed by Laurie & Jones (1938) who recorded 103 species, including 13 species in the animal groups Oligochaeta, Mollusca, Crustacea and Vertebrata, leaving 90 species belonging to animal groups tolerant of metallic pollution. Of these, a considerable number may be classified as lentic species, and it is interesting to note that many are species not strictly characteristic of the lower reaches of rivers, but more usually found in stagnant pools. In this category we may include *Polycelis nigra*, *Pyrrhosoma nymphula*, *Agrion puella*, *Notonecta glauca*, *Sialis*, *Haliplus ruficollis*, *Coelambus inaequalis*, *Hydroporus pictus*, *H. palustris*, *H. vittula*, *H. erythrocephalus*, *Illybius ater*, *Agabus bipustulatus*, *A. sturmi*, *Colymbetes fuscus*, and *Dytiscus marginalis*. All these species are absent from, or rarely found in the lower reaches of the Teifi, where the fauna tends to be limited much more strictly to species characteristic of running water. This suggests that when the Rheidol became repopulated after the long period when it was almost devoid of animal life, a number of the species which constitute its present fauna were recruited from the numerous stagnant pools nearby, and the fact that this tendency is especially evident in the case of the Odonata and Coleoptera, insects whose migration is facilitated by their power of flight, would be readily understandable. It is possible that a careful comparison of the fauna of the lower Rheidol and that of the standing waters in the valley will provide further evidence to support this theory.

4. SUMMARY

1. This paper deals with the river Teifi, the longest river running into Cardigan Bay. The river has suffered little or no pollution of any kind and possesses a rich fauna and flora. The mainstream, from its source to its estuary, measures about 80 miles and varies to a very great extent in gradient. Near its source the stream has a gradient of over 350 ft.

per mile, while in the region of the Tregaron bog the river consists of a series of stagnant pools and has a gradient of less than 2 ft. per mile.

2. Tributaries are numerous, and most of the river valley has a high rainfall, so that the river is subject to heavy floods sometimes of long duration. Most parts of the river, and particularly its middle reaches, carry a luxuriant flora, the phanerogamic vegetation appearing to be far richer than that of other rivers of the district. The river water is soft and slightly less acid than that of the rivers Rheidol, Ystwyth and Dovey.

3. For a faunistic survey the river has been divided into five regions in which samples were taken at various times over a period of two years. The fauna list includes some 147 species, the majority being Arthropoda. In accordance with the great extent to which the gradient of the mainstream varies from place to place the general nature of the fauna is very variable, ranging from a purely lotic type in the upper reaches of the river to a purely lentic type in the Tregaron bog region, while the middle and lower reaches have both types of fauna represented. The river is one of the finest fishing rivers of Wales, providing excellent fishing for salmon, sea-trout and trout, but no coarse fish are caught.

4. The fauna of the lower reaches of the Teifi is compared with that of the lower reaches of the Rheidol, a river which has become repopulated after many years of barrenness due to pollution by lead and zinc. It is shown that the fauna of the lower reaches of the Teifi is virtually limited to species generally found in flowing water, whereas that of the lower reaches of the Rheidol includes a number of species most usually found in stagnant waters. This would suggest that when the Rheidol became repopulated, a number of the species composing its present fauna were recruited from the pools in its valley.

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ECOLOGICAL STUDIES OF THE COMMONER SPECIES OF BRITISH CORIXIDAE

By E. J. POPHAM

CONTENTS

1. INTRODUCTION

Although the Corixidae (Hemiptera, Heteroptera) are to be found in almost any pond and pool throughout the country, yet very little has been written about the factors responsible for the distribution of the various species. By far the most important paper is that of Macan (1938) who has made a detailed analysis of a large number of habitats in the Lake District, and shown that there is a close relationship between the percentage of organic matter in the soil (% o.m.s.) and the species of Corixids living there. On a previous occasion the writer (Popham, 1941) has shown that certain species of Corixidae not only vary in colour, but that they tend to agree with that of the pond in which they occur. This agreement was thought to be due to the following factors:

(1) the action of predators in destroying those insects not adapted to the background;

(2) the action of the background in controlling the intensity of pigmentation of nymphs and young adults, and

(3) choice by the adults of a background with which they harmonize.

Studies on the last two are recorded in the present paper.

At the time of writing (1942), the classification of the Corixidae is in a state of flux. Mr China of the British Museum has drawn my attention to a classification by Walton (in Hutchinson, 1940) who has divided the genus '*Corixa*' into some nine subgenera; but until this system has been confirmed by other authorities, it has been decided to follow the nomenclature of Macan (1939). The generic name '*Arctocorisa*' is therefore used for '*Sigara*'.

The Ostwald Colour Chart has again been used as a standard and the percentages of white in the various standards are:

'a'	'b'	'c'	'd'	'e'	'f'	'g'	'h'
89	71	56	45	35	28	22	18
'i'	'k'	'l'	'm'	'n'	'o'	'p'	
14	11	8·9	7·1	5·6	4·5	3·5	

The colours of the insects and ponds are given at their grey value.

2. THE DEVELOPMENT OF PIGMENTATION

It has previously been shown (Popham, 1941) that the 'colour acquired by a nymph or young adult' of *Sigara distincta* 'depends directly upon the colour of the environment in which it has lived during the process of moulting'. This fact has been confirmed in subsequent experiments, and in addition two lines of study have been followed: (*a*) the influence of heredity in the development of pigmentation, and (*b*) the factors responsible for the control of pigmentation.

(*a*) *The influence of heredity in the development of pigmentation*

The experiments under this heading were performed in four small aquaria, measuring 10 × 8 × 8 in. and filled with pond water to a depth of 7 in. Two aquaria were lined with silver sand (coloured '*e*') and the other two were lined with emery powder (coloured '*n*'). Protozoal and algal infusions were added to act as food. All four aquaria were kept close together so that they should have the same temperature and illumination. Specimens of *S. distincta* in copula were collected from a local pond,

and then sorted according to colour. Six pairs, all coloured '*i*', were added to one of the aquaria containing silver sand and also to one containing emery powder. Into each of the two other aquaria was added six pairs, all coloured '*n*'. Soon eggs appeared, and of those which hatched a number lived as far as the third instar. The experiment was then stopped and the colours of the nymphs in the various aquaria were recorded in Table 1.

Table 1. *The colour of third instar nymphs bred in the aquaria indicated*

Exp.	Colour of parents	Colour of background	No. of eggs	Colour of nymphs *n–l*	*l–i*	*i–g*
1	*n*	*n*	112	18	6	4
2	*n*	*e*	146	1	4	24
3	*i*	*n*	86	23	8	5
4	*i*	*e*	132	1	5	28

The similarity between the results of Expts. 1 and 3 and between 2 and 4 shows that the colour of the background is more important than genetical factors in determining the colour of the nymphs. If these experiments had been performed on a larger scale, and the nymphs had been bred to maturity, it might have been possible to demonstrate the presence of genetical factors in controlling pigmentation. However, it seems very improbable that one set of factors should act in the nymph and another set in the adult, and previous experiments performed by the author did not in any way suggest that this was the case.

(*b*) *Factors controlling the development of pigmentation*

Giersberg (1928) and Schlottke (1934) have shown that high temperatures encourage the formation of melanin, and the same for humidity has been demonstrated by Mell (1931) and Faure (1932). Melanin pigmentation also appears to be encouraged by ultraviolet light, the influence of which takes place through the eyes (Brecher, 1924). Atzler (1930) had previously shown that the colour change in *Dixippus* is controlled through the eyes, and that section of the eye stem eliminates this response. Before attempting to discover the factors responsible for the control of pigmentation, it was first necessary to determine the influence of the background upon the development of pigmentation after the process of moulting had taken place. Accordingly nymphs of *Sigara fossarum* were collected and kept for at least 3 days on background '*i*'. As soon as moulting had occurred, the young adult was transferred immediately to one of two tanks coloured '*a*' or '*n*'. The colour of the adults after 6 and 12 hr. is recorded in Table 2.

Table 2. *Colour attained by young adults of* Sigara fossarum *when reared on the backgrounds indicated*

Exp.	Colour of background	Colour of adults *n–l*	*l–i*	*i–g*	Time from moulting hr.
1	*a*	2	16	14	6
	n	4	25	6	
2	*a*	2	21	9	12
	n	4	25	6	

The results of Table 2 show that while the final colour attained by the young adults is unaffected by the colour of the background after moulting, yet it would appear that the rate at which the pigment is deposited is to some extent influenced by it.

A second experiment was then performed by the same method, except that the eyes of the newly formed adults were covered with black cellulose paint. It was found that the paint dried within a matter of seconds, and that provided the skin was quite dry it was unaffected by the water and did not wear off. The colour attained by the adults at the end of 6 hr. is given in Table 3.

Table 3. *Colour attained by newly hatched adults reared on backgrounds '*a*' and '*n*' with their eyes blacked out*

Colour of background	Colour of insects *n–l*	*l–i*	*i–g*
a	—	2	18
n	—	1	15

It will be seen that the control of pigmentation takes place through the eyes, and when these are blacked out the control disappears. In view of the pale colour acquired by the insects, it would appear that the rate at which melanin is deposited is proportional to the difference between the intensity of light falling on the dorsal surface of the eye and that reflected from the background. It was subsequently shown that the nervous system is mainly responsible for controlling the deposition of melanin, for when the nerve cord of newly hatched adults was cut, the control of pigmentation likewise disappeared. In this third experiment care was taken to cut the ventral nerve cord in the cervical region with a very thin knife which was driven vertically upwards, until the point was felt in the mid-dorsal surface. In this way it was possible to leave the blood supply to the head unimpaired. It was therefore possible to discover if the controlling factors were due to the nervous system or to a hormone secreted in the head. The results of this third experiment, which was done by a similar method to that of the first, are recorded in Table 4.

Table 4. *Colour attained by young adults with a severed nerve cord*

Colour of background	Colour of insects *n–l*	*l–i*	*i–g*
a	—	13	7
n	—	11	9

Decapitated insects darken after moulting owing

to the presence of enzymes already deposited in the skin. These experiments show therefore that the deposition of melanin in the skin after moulting is under the control of the nervous system, and that the colour of the background is perceived through the eyes. It is well known that most Hemiptera show a distinct tendency to become darker with age. Careful experiments have been performed several times to see if this phenomenon also occurs in the various species of *Sigara*, but negative results have always been obtained, and the final colour of the adult is usually acquired within 24 hr. of moulting.

3. THE COLOUR OF THE HABITAT

Brown & O'Neal (1923) have shown that the colour of a soil darkens with the humus content, while Simon (1929, 1930) has demonstrated the importance of mineral salts in modifying the colour. Observations of other authors have shown that the colour of a soil is first determined by that of the particles of rock and then secondarily darkened by the amount and type of organic matter present. In aquatic habitats with a high percentage of organic matter, there is a wide range of colour which seems mainly to depend upon the degree of decomposition which has occurred. Where very little change has taken place, the soil is often coloured approximately '*l*', but a very dark colour ('*o*'–'*n*') is obtained when the humus is decomposed into a colloidal mass of organic matter in which little or no trace of plant structure can be detected.

Table 5*a*. *The range of colour of some of the common species and the range of colour of the habitats in which they occur*

Species	Range of colour of species	Range of colour of habitats
Sigara sahlbergi	*o–l*	*o–l*
S. linnei	*o–l*	*o–i*
S. castanea	*o–g*	*o–i*
S. striata	*o–g*	*o–g*
S. falleni	*o–i*	*o–g*
S. distincta	*o–g*	*o–g*
S. fossarum	*o–i*	*o–h*
S. scotti	*o–g*	*o–g*
S. nigrolineata	*o–e*	*o–e*
S. praeusta	*o–i*	*o–i*
S. wollastoni	*o–g*	*o–i*
Cymatia bonsdorffi	*o–i*	*o–i*
Corixa punctata	*o–i*	*o–i*
Micronecta poweri	*l–e*	*l–e*

(Details of the collections are given in the Appendix.)

In 1938 and 1939, Macan published an account of the general type of habitat preferred by each of the British species of Corixidae, and though he confines himself to factors of a chemical and physical nature, there are indications that the colour of the pond might also be of some importance. For example, *Sigara sahlbergi* and *S. linnei* are described as occurring in 'woodland pools with the bottom covered with dead leaves', that *S. striata* occurs 'particularly where the bottom is sandy', and *S. nigrolineata*, which has a great range of pigmentation, is described as being 'common and widespread'. Collections were made from some seventy-five ponds in Surrey, Lancashire and Westmorland in order to determine if any relationship exists between the range of colour of any species and that of the habitats in which it is to be found. The colours of the habitat and the insects were recorded and are given in Tables 5*a* and 5*b*, which gives the range of colour of any species and that of the ponds and lakes from which it was collected.

One of the advantages of using the Ostwald Colour Chart is that each standard differs from adjacent ones by the same apparent contrast. It is therefore possible to give the numerical values of 3, 2, 1 and 0 to standards '*n*', '*l*', '*i*' and '*g*' respectively and thence to calculate the average colour of the specimens of each species collected from any one habitat. These averages are given in the Appendix, and from them was calculated the correlation between the colours of the individuals of any one species and those of the ponds from which they were obtained. *Cymatia bonsdorffi*, *Sigara castanea* and *S. nigrolineata* have been omitted from Table 5*b* because collections were made only from so small a number of habitats. The correlations are given in Table 5*b*.

It is possible to extract from the tables in the Appendix, the frequency with which any species occurs on a particular type of background, and the results are given in Table 6.

Table 5*b*. *Correlation between the colours of any one species and those of the ponds in which they occur*

Species	Correlation	*n*–2	Species	Correlation	*n*–2	Species	Correlation	*n*–2
Sigara sahlbergi	0·45	8	Sigara distincta	0·73	27	Sigara wollastoni	0·89	9
S. linnei	0·62	23	S. fossarum	0·79	18	S. praeusta	0·74	9
S. striata	0·69	14	S. scotti	0·74	21	Micronecta poweri	0·88	10
S. falleni	0·88	11						

In the above table '*n*' = no. of habitats examined.

If Table 6 is analysed it is possible to arrange the various species in series according to the average colour of the background on which they occur, beginning with the lightest:

Micronecta poweri	S. scotti and fossarum
Sigara striata	S. linnei and praeusta
S. falleni	Cymatia bonsdorffi
S. distincta and castanea	Sigara sahlbergi

The succession for the % o.m.s. as observed by Macan (1938) is as follows:

Micronecta poweri
Sigara striata
S. distincta and fossarum
S. scotti
S. castanea and Cymatia bonsdorffi
Sigara linnei

The reason for the similarity in these two series, is, as has previously been explained, that the colour of the soil is, to a large extent, influenced by the quantity of organic matter present. The differences in the two series arise because Macan only considered the quantity of organic matter present, but with soils containing a high percentage of organic matter, the degree of decomposition is probably more important. For example, *Sigara fossarum* and *Cymatia bonsdorffi* occur partly on soils where the organic matter has reached an advanced stage of decomposition. In a similar way *Sigara castanea* appears in a relatively higher position in Macan's table because this species prefers those soils where decomposition has only just begun, and therefore the colour of the soil is mainly determined by the presence of large quantities of undecomposed organic matter, which is, therefore, relatively pale in colour.

Table 6 also gives a clue to the differences in the distribution of *S. nigrolineata* and *S. wollastoni*. Both these species, according to Macan, occur in high pools where there is a high percentage of organic matter. *S. wollastoni* seem far more tolerant of the black colloidal peat than *S. nigrolineata* and therefore is to be found in those pools where the organic matter has reached an advanced degree of decomposition.

In a general way the colour of a habitat is proportional to the quantity of organic matter present, and this is why there is a close resemblance between the two series given above. The distribution of each species will be discussed later in § 5 of this paper.

Table 6. *The number of habitats of the colour indicated in which Corixids were found*

	Colour of habitat								
Species	*o–n*	*n–m*	*m–l*	*l–k*	*k–i*	*i–h*	*h–g*	*g–f*	*f–e*
Sigara sahlbergi	3	4	3	0	0	0	0	0	0
S. linnei	6	6	5	3	5	0	0	0	0
S. praeusta	2	4	2	2	1	0	0	0	0
S. castanea	1	2	4	2	1	0	0	0	0
S. striata	2	3	1	1	3	3	3	0	0
S. falleni	2	3	2	2	2	1	1	0	0
S. distincta	7	6	7	3	4	2	0	0	0
S. fossarum	4	8	3	3	1	1	0	0	0
S. scotti	4	6	5	5	2	1	0	0	0
S. nigrolineata	4	2	3	0	0	1	1	0	1
Cymatia bonsdorffi	1	2	4	0	1	0	0	0	0
Sigara wollastoni	6	2	0	2	1	0	0	0	0
Micronecta poweri	0	0	0	3	2	2	2	1	2

4. THE MIGRATION OF CORIXIDAE

Macan (1938) has recorded that the Corixidae migrate from one habitat to another, and similar observations have been made by other authors, but there is very little detailed information. The following experiment was performed in order to discover which species most readily took to flight. Four freshly collected specimens of fourteen common species were placed in a large shallow dish, 20 × 15 in., and lined with sand coloured '*i*'. The dish was partly filled with water and then tilted so as to leave a small patch of dry sand at one end. As each insect flew out of the dish it was recaptured and identified. Observations showed that the fourteen species chosen could be divided into three more or less distinct groups as follows:

(*a*) Those species which readily took to the wing within 5 min.

Sigara nigrolineata	Sigara sahlbergi
S. wollastoni	Corixa punctata

(*b*) Those species which migrated within 30 min. of the start of the experiment.

Corixa dentipes	Sigara striata
Sigara falleni	S. praeusta
S. distincta	S. linnei

(*c*) Those species which did not readily take to flight.

Sigara castanea	Sigara scotti
S. fossarum	Cymatia bonsdorffi

(*a*) *Emigration of Corixidae*

Although Macan (1938) made no direct observations on the factors which are responsible for initiating migration, yet, inasmuch as he has shown that there is a very close relationship between the % o.m.s. and the species living there, it can be assumed that the quantity of organic matter present is an important factor in stimulating the migration of a particular species.

As the Corixids seem to be detritus feeders it is difficult to say whether or not this factor can be regarded as one of nutrition. The digestive tracts of a large number of Corixids have been examined, and in no specimen was it ever possible to discover any organic remains which could be identified.

The writer (1941) has previously shown that when *S.* (*Arctocorisa*) *distincta* is placed on a background with which it does not harmonize it becomes restless and attempts to migrate. It was also shown that when the insects are crowded together in a small tank, migration occurs more readily than when the insects are given more space. Experiments to determine if migration is initiated by the *p*H of the water gave only negative results. Although in nature, Corixids are rarely found in ponds with a *p*H lower than 5 or in alkaline habitats with a *p*H higher than 9, yet *S. distincta* showed no abnormal tendency to migrate when kept for 12 hr. in water with a *p*H of 3 or 11. In another experiment fifteen specimens were placed in a trough containing slowly moving water, when twenty-six migrations were observed in 10 min.; whereas only twelve attempts were made in the same time when the water was still.

Table 7. *The number of migrations made in 15 min. by specimens of* Sigara distincta *at different temperatures*

Temp. °C.	No. of migrations
15	0
20	2
25	6
30	22
35	5

The effect of temperature in initiating migration was clearly shown by placing twelve specimens of *S. distincta* in a white dish 10 × 8 in. filled with water to a depth of 1 in. The temperature of the water was carefully controlled and the number of insects which migrated in 15 min. was recorded. As soon as any insect flew out, it was recaptured and replaced in the dish. The number of migrations are recorded in Table 7.

At 15° C. none of the insects attempted to migrate, but as the temperature was raised the insects became more and more active, until at 30° C. twenty-two migrations were recorded. It was found impossible to continue the experiments above 35° C. as the insects tended to die at these high temperatures. The conclusions of these experiments were confirmed by observations made at Little Ludderburn Tarn which is a very shallow pond, the bottom of which is uniformly lined with decaying organic matter. On 31 July 1942 it was observed that in one or two places near the edge, parts of the pond had become isolated and that the temperature of the water here was from 25° C. upwards. Careful observations were made and these isolated regions were found to be completely devoid of Corixids, whereas another patch, only a few yards away which was kept at a temperature of approximately 14° C. by the presence of a small stream, was found to contain large numbers of these insects.

Macan (1938) states of *Micronecta poweri* that 'this insect was...found in large numbers at depths of 2 and 3 ft.' Apart from this record, very little seems to be known of the optimum depth of water at which the various species of the Corixidae occur. Collections were therefore made at five different habitats, where conditions were sufficiently uniform to permit collections being made from a number of depths. The number of insects captured in twenty standard sweeps with a hand net is recorded in Table 8.

Table 8 shows that *S. striata*, *S. distincta* and *S. fossarum* are commonest in water less than a foot in depth. Collections made at Royshaw Quarry, Blackburn, Lancashire, throughout the year suggest that Corixids migrate into shallow water during fine sunny weather, and that this migration is not necessarily related to the temperature as these insects may be seen in large numbers under the ice on bright days. Observations on *Micronecta poweri* showed that this insect is commonest at a depth of about 2 ft., and it would appear that the presence of the other Corixids in such shallow water is mainly due to the occurrence of detritus there, while *M. poweri*, which dislikes large quantities of organic matter, is only able to find a suitable habitat by living at a greater depth where such humus does not normally collect.

Table 8. *The numbers of* Sigara *captured with twenty standard sweeps of a hand net at different depths*

Habitat	Brathay Bar	Clay Pond	Pull Wyke Stream (1)	Pull Wyke Stream (2)	Congo Mouth
Commonest species ...	*S. striata*	*S. fossarum*	*S. distincta*	*S. distincta*	*S. distincta*
Depth (ft.)					
0·5	246	205	196	235	116
1·5	28	19	5	58	12
2·5	3	0	0	3	0
3·5	0	—	—	—	—

It would therefore appear that as a pond dries up, the increased temperature together with the increasing population density of the Corixids are probably the main factors in initiating migration. It was observed that fifteen specimens of *Corixa punctata* migrated in 10 min. from a trough containing water to a depth of ½ in., and that no migrations took place in 6 hr. when the depth of water was increased to 1 ft. 3 in.

It has previously been shown (Popham, 1942) that submerged Corixids do not orientate themselves to light, but that on leaving the water they are first negatively heliotaxic until the wings have dried, when they become positively heliotaxic, and eventually fly towards the light. The influence of wind is a factor which does not readily lend itself to quantitative analysis, but observations on a number of specimens released at various times have shown that a very slow wind of some 5–10 m.p.h. is sufficient to blow even the heaviest of Corixids out of their course. It is perhaps of no little significance that alpine species such as *Sigara nigrolineata* and *S. wollastoni* should be among the smallest of the Corixids.

(*b*) *Immigration of Corixidae*

It is well known that the number of Corixids varies considerably from one habitat to another. There must be so many factors concerned in controlling the numbers of Corixids that it is only possible to discuss a few of them. As yet nothing is known of the reproductive rates of the various species, though it would seem improbable that variations in these could, of themselves, account for the variations in numbers. It is known, for example, that open-air swimming baths quickly become infested with Corixids, showing that their abundance is mainly due to migration. If a habitat is unsuitable for any particular species it will migrate, only to be replaced by others. It has already been shown that the Corixidae are able to colonize a very wide range of habitats, so that the numbers of Corixids present must to no small extent be determined by the immigration rate of these species. For this reason, if collections are made from a large number of habitats in which Corixids occur, the population density may give some indication of the number of insects arriving there, and also those types of pond to which Corixids are most attracted.

Collections were made from some thirty ponds in various parts of Surrey, Lancashire and Westmorland. For each habitat was recorded (1) the number of Corixids captured in ten standard sweeps of a net, (2) its general features, position, surroundings, etc., and (3) the species occurring in the largest numbers. All collections were made in August 1941.

While the above records were being made, it became obvious that the number of Corixids obtained might vary considerably in one habitat. On warm sunny days the insects were exceptionally common, and less so when the weather was colder, or the sky was overcast. For these reasons, collections were completed within a fortnight during August 1941, when a spell of fine weather made conditions more or less uniform. Also, as a high record cannot be spurious, several collections were made for each pond, and only the highest is given in the table. A study of Table 9 shows that those ponds with the highest numbers of insects have the following features in common:

(*a*) They are not surrounded by trees, buildings, etc., and if they occur in a quarry its sides are neither steep nor very high.

(*b*) They are often in the middle of fields.

(*c*) They are often near the summit of a hill, or on the side with the prevailing wind.

(*d*) They have relatively little vegetation.

(*e*) They are fairly large and lined with fine sand or mud.

In contrast, ponds such as Rose Castle Tarn, Slew Tarn, etc., are smallish and overhung with trees, which shelter them from the prevailing wind. It will therefore be seen that the immigration of Corixids to a pond is mainly determined by the ease with which it can be found, so that ponds in a prominent position have a higher immigration rate than those which are hidden in a quarry or a wood. Small ponds surrounded by trees contain few Corixids, because they are hidden from migrating insects, and the high % o.m.s. produced by the leaves make them suitable only for a restricted number of species. On the other hand, though Lake Windermere must receive a very large number of Corixids, yet these insects occur in large numbers only in those bays where a sufficiently high percentage of organic matter can collect.

5. NOTES ON THE ECOLOGY OF SOME OF THE COMMONER SPECIES

Cymatia bonsdorffi (C. Sahlb.) has very poor powers of flight and is mainly restricted to dark soils containing a high % o.m.s. where the organic matter has reached an advanced stage of decomposition.

Corixa punctata Illig. (*geoffroyi* Leach) occurs in temporary habitats which are rarely above 1500 ft. Its powers of flight are considerable and it takes to the wing fairly readily. It has a range of colour from '*o*' to '*i*' and is therefore able to colonize a variety of habitats.

Corixa dentipes (Thoms.) seems to have a similar distribution to that of *C. punctata*.

Corixa affinis Leach occurs in large numbers in Kingsmere, Wimbledon Common, Surrey, and in a few surrounding ponds. The specimens collected from these habitats were pale in colour which varied from '*i*' to '*g*'; they were found on sandy or clay bottoms which had a very low % o.m.s. and contained no other vegetation than occasional masses of *Spirogyra*. The water was slightly alkaline (*p*H 9·5). *Corixa affinis* does not readily take to flight and in Kingsmere was associated with *Sigara limitata*.

Sigara limitata (Fieb.) has a restricted range of colour '*i*' to '*e*' and is found on pale backgrounds containing very little organic matter in the soil. This species seems to prefer alkaline habitats, and does not readily take to flight.

Sigara sahlbergi (Fieb.) occurs in dark habitats where there is a high percentage of organic matter,

Its presence in woodland pools lined with dead leaves would suggest that it avoids those habitats where the organic matter has reached an advanced stage of decomposition. It readily takes to the wing, a feature which seems correlated with its small range of habitat.

Sigara linnei (Fieb.) has a similar distribution to that of *S. sahlbergi*, except that the range of colour of its habitats is rather wider, and it takes to the wing less readily. Macan (1938) has shown that these two species are the last to occur in a pond where the rock, but instead by the large quantities of plant remains which occur there.

Sigara striata (Linn.). Though this species has a wide range of colour, a study of the records given in the Appendix will show that it does not easily adapt itself to the darker habitats. It is commonest in habitats where the bottom is sandy, and on account of the small % o.m.s. these are usually very pale in colour. This species has also been found in large numbers in E.W.S. tanks in London where the % o.m.s. is very low.

Table 9. *The number of Corixids collected in ten standard sweeps of a net from various ponds*

Name of habitat	No. of Corixids captured	Commonest species	Size of pond	Position	Surroundings
Wray Mires	156	Sigara castanea	M	H	t
Blelham Tarn	152	S. fossarum	L	V	—
Royshaw Quarry	140	S. distincta	M	H	q
Clay Pond	138	S. fossarum	S	H	—
Wise Een Tarn	134	S. scotti	L	H	—
Duck Tarn	128	S. linnei	M	H	—
Wray Mires (2)	97	S. castanea	M	H	T
Bank Hey, Blackburn	78	S. striata	M	H	—
New Tarn	76	Cymatia bonsdorffi	M	H	—
Kingsmere, Surrey	75	Sigara distincta	M	H	—
Barngates Quarry	74	S. castanea	S	H	q
Pond B, Blackburn	67	S. distincta	S	H	q
Congo Mouth	48	S. distincta	S	V	t
Wilpshire Quarry	46	S. wollastoni	S	V	Q
Pull Wyke Stream	40	S. falleni	L	V	t
Robinson's Tarn	34	S. castanea	M	H	T
Waterhead Bay	32	S. striata	L	V	—
Wray Mires Fish Ponds (1)	26	S. scotti	S	H	—
Wray Mires Fish Ponds (3)	14	S. scotti	S	H	t
Queensmere, Surrey	13	S. distincta	M	V	T
Slew Tarn	13	S. linnei	M	V	T
Cunliffe Quarry	12	S. distincta	S	H	Q
Pond A, Blackburn	10	S. distincta	S	H	—
Close Brow Quarry	9	S. sahlbergi	S	V	Q
Whitecross Creek	8	S. striata	S	V	T
Lost Tarn	4	S. fossarum	M	V	T
Lindeth Tarn	3	S. scotti	S	H	—
Rose Castle Tarn	1	S. praeusta	S	V	T
Pond C, Blackburn	1	S. praeusta	S	H	Q

Key to Table 9

Size of pond: L = large, M = medium size, S = small.
Position: H = near or at the top of a hill, V = in a valley.
Surroundings: Q = pond in a deep quarry, q = pond in a shallow quarry, T = surrounded by trees on all sides, t = surrounded by trees on one side only.

% o.m.s. is slowly increasing. It might also be said that as the colour darkens these two species are liable to appear when the background becomes darker than '*l*'.

Sigara castanea (Thoms.) occurs in habitats containing a high % o.m.s., yet the range of colour of its habitats is much paler than that of the last two species. The reason for this is that *S. castanea* is commonest on soils where the organic matter has only partly decomposed. The colour of such soils is not first determined by the colour of the particles of

Sigara distincta (Fieb.) and *Sigara falleni* (Fieb.). These two species have a similar distribution. Both have a wide range of habitats, though those of *S. falleni* tend to be slightly paler than those of *S. distincta*. Both species take to flight fairly easily, a factor which is probably responsible for their wide distribution.

Sigara nigrolineata (Fieb.) has an exceptionally wide range of colour. It is to be found in a variety of habitats ranging from dark peat pools to the pale cement of an ornamental pond. It is commonest in

small pools of a temporary nature, and correlated with this is the extreme readiness with which it takes to wing. Its small size makes it liable to being carried by the wind to subalpine pools from which it may be collected in almost any part of the Lake District.

Sigara fossarum (Leach) is often associated with *S. distincta* and occurs in habitats containing a moderate quantity of organic matter. However, the range of colour of its habits seems to be slightly darker than *S. distincta*, showing that it prefers soils where the organic matter has reached an advanced stage of decomposition.

Sigara scotti (D. & S.). This species occurs in habitats with a wide range of colour and in the % o.m.s. It does not readily take to flight, a factor which probably accounts for its success in becoming the dominant species of a very large variety of habitats in the north.

Sigara praeusta (Fieb.) is commonest in habitats coloured '*n*'–'*l*', and as the tables in the Appendix will show, it does not easily adapt itself to pale habitats. It occurs, therefore, in habitats where there is a high % o.m.s. and where the humus has undergone a moderate degree of decomposition.

Sigara wollastoni (D. & S.) is commonest in peaty pools above 1500 ft. containing a high percentage of organic matter. It has a darker and more restricted range of habitats than *S. nigrolineata*, showing that it is more tolerant of soils where the organic matter has reached an advanced stage of decomposition. It is more successful in establishing itself, and related to this is the fact that it does not take to the wing as readily as *S. nigrolineata*. It is essentially a northern species.

Var. *caledonica* (Kirk.). This variety, which occurs in Loch Leven and a few of the other Scottish lakes, is a variety of *S. wollastoni* which it closely resembles in having the same genitalia and in several other features. Macan (1939) states that it is slightly smaller than *S. wollastoni* and has narrower and straighter dark markings. *S. caledonica* is usually described as being very pale in colour. Unfortunately, it has only been possible to examine the British Museum collections of dried specimens. In the Power collection, which was made about 1888, the darkest specimen is only coloured approximately '*g*'; but as the whole collection seems to have faded, this probably has little significance. In the Butler Collection of 1936–7 the specimens are very much darker, and here the specimen with the deepest pigment is coloured approximately '*l*'. Even in those species which show a wide range of pigmentation, such as *S. nigrolineata*, a certain degree of variation in the thickness and shape of the dark lines is to be observed, and it would appear that the difference in colour between *S. wollastoni* and *S. caledonica* may have no more significance than the variation of pigmentation of the other species; but before a definite decision can be reached, it will first be necessary to examine a large number of living specimens, and to perform experiments with a view to inducing the formation of dark pigmentation.

Sigara carinata (C. Sahlb.). Only a few specimens of this species have been obtained, all of which were very dark in colour and were collected from a dark peat pool where the humus had reached a very advanced stage of decomposition.

Sigara germari (Fieb.). The few specimens of this species were collected from a sandy habitat coloured '*i*'–'*g*', and the insects were of the same colour.

Micronecta poweri (D. & S.) is an exceptionally small species which was collected from the shores of the north basin of Lake Windermere, where the soil was very sandy or where there was a layer of submerged moss. This species chooses those soils which contain a very low percentage of dead organic matter, and hence these insects are to be found in deep water where the humus and detritus does not collect. Its range of colour as well as that of its habitats is very much paler than any other species of Corixidae. Its presence on rocks which are covered with a thin layer of algal growth would suggest that it does not feed on organic detritus to the same extent as the others.

From the accounts of the above species, three main types of distribution are to be found.

First, in such species as *S. distincta* and *S. scotti* there is a wide range of pigmentation and the insects are able to colonize a variety of habitats. These species do not readily take to the wing and are usually present in large numbers in those habitats in which they occur.

A second type of distribution is to be found in *Corixa punctata*, *Sigara nigrolineata* and perhaps to a lesser extent in *S. wollastoni*. These species have a very wide range of pigmentation and readily take to the wing, and are found in various types of habitat which are usually only of a temporary nature.

Finally, in *S. sahlbergi*, *S. striata* and *Micronecta poweri* there is a restricted range of pigmentation and a corresponding restricted variety of habitats. It is interesting to note that of these three species only *Sigara sahlbergi* takes readily to the wing, a factor which is probably related to the rareness of the dark habitats it prefers.

S. linnei occupies an intermediate position between *S. sahlbergi* and *S. distincta*, both with regards to its variation in pigmentation and its readiness to migrate.

From the evidence supplied by *S. wollastoni* it would appear that a species with a wide range of habitats tends to become divided into at least two sections, one of which restricts itself to the paler background (var. *caledonica*) while the other is to be found mainly on the darker habitats. This line of evolution could arise by the simple process of isolation, for, as the writer has previously shown (Popham, 1943), there is evidence that in the Corixidae the males tend to choose as a mate a female either the same colour as themselves or else slightly lighter.

6. SUMMARY

1. The final colour acquired by a nymph or young adult *Sigara* depends on the colour of the background on which it was reared before moulting. The development of pigmentation is under the control of the nervous system acting through the eyes.

2. There is a high correlation between the range of colour of any species of Corixidae, and that of the habitats in which it occurs in nature.

3. Adult Corixidae are mainly stimulated to migrate by high temperatures, overcrowding, and an unsuitable background.

4. Ponds receiving the largest number of Corixidae are those which are not concealed by their surroundings.

5. Ecological notes on the distribution of the commoner species are given at the end of this paper.

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APPENDIX

Records of collections made for each of the species indicated

Numbers in brackets indicate the number of the station in the various habitats

In the following tables the various standards of colour are given the numerical values indicated:

o	3·5	*m*	2·5	*k*	1·5	*h*	0·5	*f*	−0·5
n	3·0	*l*	2·0	*i*	1·0	*g*	0·0	*e*	−0·1

After each named habitat the following abbreviations are used to indicate the county in which they occur:

NL	North Lancashire (Lake District).	C	Cumberland.
SL	South Lancashire (Ribble Valley).	S	Surrey.
W	Westmorland.		

* = not mapped by Macan (1938).

Habitat		Colour of habitat: Between standards	Colour of habitat: Between values	Colour of insects: *o–m*	Colour of insects: *m–k*	Colour of insects: *k–h*	Av. colour of insects
		Sigara praeusta					
Duck Tarn (1)	NL	*o–n*	3·5 and 3·0	4	—	—	3·0
Barngates Quarry	NL	*o–n*	3·5 and 3·0	9	—	—	3·0
Slew Tarn (1)	NL	*n–m*	3·0 and 2·5	13	1	—	2·9
Slew Tarn (2)	NL	*n–m*	3·0 and 2·5	3	1	—	2·75

Habitat		Colour of habitat: Between standards	Colour of habitat: Between values	Colour of insects: o–m	Colour of insects: m–k	Colour of insects: k–h	Av. colour of insects
		Sigara praeusta					
Duck Tarn (2)	NL	*n–m*	3·0 and 2·5	5	3	1	2·4
Royshaw Quarry (1)	SL	*n–m*	3·0 and 2·5	6	2	—	2·75
Duck Tarn (3)	NL	*m–l*	2·5 and 2·0	6	—	—	3·0
Lindeth Tarn	W	*m–l*	2·5 and 2·0	15	—	—	3·0
Slew Tarn (4)	NL	*l–k*	2·0 and 1·5	3	10	—	2·2
Royshaw Quarry (2)	SL	*l–k*	2·0 and 1·5	1	4	—	2·2
New Tarn	W	*k–i*	1·5 and 1·0	1	2	1	2·0
		Sigara sahlbergi					
Slew Tarn (3)	NL	*o–n*	3·5 and 3·0	4	—	—	3·0
*Pond 'B' Yellow Hills	SL	*o–n*	3·5 and 3·0	12	—	—	3·0
*Five Bar Gates Quarry (3), Blackburn	SL	*o–n*	3·5 and 3·0	25	—	—	3·0
Wise Een Tarn (1)	NL	*n–m*	3·0 and 2·5	2	3	—	2·4
Wise Een Tarn (3)	NL	*n–m*	3·0 and 2·5	1	—	—	3·0
Duck Tarn (2)	NL	*n–m*	3·0 and 2·5	2	—	—	3·0
*Cunliffe Quarry, Blackburn	SL	*n–m*	3·0 and 2·5	8	—	—	3·0
*Wilpshire Quarry, Blackburn	SL	*m–l*	2·5 and 2·0	15	3	—	2·8
Duck Tarn (3)	NL	*m–l*	2·5 and 2·0	2	—	—	3·0
*Cherry Tree Quarry, Blackburn	SL	*m–l*	2·5 and 2·0	2	—	—	3·0
		Sigara linnei					
Duck Tarn (1)	NL	*o–n*		5	—	—	3·0
Slew Tarn (5)	NL	*o–n*		3	1	—	2·75
Barngates Quarry	NL	*o–n*	3·5 and 3·0	9	1	—	2·9
Slew Tarn (4)	NL	*o–n*		10	1	—	2·9
Wray Mires (3)	NL	*o–n*		11	—	—	3·0
Wray Mires (1)	NL	*o–n*		2	—	—	3·0
Wray Mires Fish Pond (1)	NL	*n–m*		11	1	—	2·9
Robinson's Tarn	NL	*n–m*		4	—	—	3·0
Wray Mires Fish Pond (2)	NL	*n–m*	3·0 and 2·5	7	—	—	3·0
Wise Een Tarn (3)	NL	*n–m*		1	—	—	3·0
Pull Wyke Swan	NL	*n–m*		1	—	—	3·0
Wray Mires (2)	NL	*n–m*		3	1	—	2·75
Barngates Quarry (2)	NL	*m–l*		2	—	—	3·0
Lindeth Tarn	W	*m–l*		9	—	—	3·0
Slew Tarn (6)	NL	*m–l*	2·5 and 2·0	3	1	—	2·75
Clay Pond	NL	*m–l*		3	1	—	2·75
Wray Mires (4)	NL	*m–l*		12	10	—	2·5
Wray Mires (5)	NL	*l–k*		6	11	2	2·2
Barngates Quarry (3)	NL	*l–k*	2·0 and 1·5	6	5	—	2·5
Wray Mires (6)	NL	*l–k*		2	4	—	2·3
New Tarn	W	*k–i*		2	—	—	3·0
Pull Wyke Stream	NL	*k–i*		8	7	—	2·5
Barngates Quarry (4)	NL	*k–i*	1·5 and 1·0	9	6	—	2·6
Clay Pond (2)	NL	*k–i*		2	5	—	2·3
*Cherry Tree Quarry (2)	SL	*k–i*		2	3	—	2·4
		Sigara castanea					
Barngates Quarry	NL	*o–n*	3·5 and 3·0	43	11	—	2·8
Wray Mires (2)	NL	*n–m*	3·0 and 2·5	30	9	1	2·7
Wray Mires Fish Pond (1)	NL	*n–m*		—	2	—	2·0
Clay Pond	NL	*m–l*		—	1	—	2·0
Duck Tarn (3)	NL	*m–l*	2·5 and 2·0	2	—	—	3·0
Slew Tarn (6)	NL	*m–l*		4	10	4	2·0
Robinson's Tarn (2)	NL	*m–l*		3	2	—	2·6
Barngates Quarry (3)	NL	*l–k*	2·0 and 1·5	19	13	2	2·5
Wray Mires (6)	NL	*l–k*		54	71	5	2·4
Barngates Quarry (4)	NL	*k–i*	1·5 and 1·0	2	9	2	2·0

Habitat		Colour of habitat: Between standards	Colour of habitat: Between values	Colour of insects: *o–m*	Colour of insects: *m–k*	Colour of insects: *k–h*	Av. colour of insects
			Sigara striata				
Duck Tarn (1)	NL	*o–n*	3·5 and 3·0	3	2	—	2·6
Congo Mouth (2)	NL	*o–n*		6	5	3	2·2
Congo Mouth (1)	NL	*n–m*		10	4	5	2·3
Pull Wyke Stream (1)	NL	*n–m*	3·0 and 2·5	4	7	4	2·0
Pull Wyke Stream (2)	NL	*n–m*		1	2	4	1·6
White Cross Creek	W	*m–l*	2·5 and 2·0	—	2	1	1·7
Brathay Bar	W	*l–k*	2·0 and 1·5	9	38	29	1·7
Pull Wyke Stream (3)	NL	*k–i*		4	8	5	2·0
Cunliffe Quarry (2)	SL	*k–i*	1·5 and 1·0	8	17	5	2·1
*Bank Hey, Blackburn	SL	*k–i*		10	21	5	2·1
Waterhead Bay (1)	W	*i–h*		6	14	27	1·5
Brathay Bar (2)	W	*i–h*	1·0 and 0·5	—	8	7	1·5
*Cherry Tree Quarry (3)	SL	*i–h*		3	7	4	2·0
Waterhead Bay (2)	W	*h–g*		1	10	33	1·2
White Cross Creek (2)	W	*h–g*	0·5 and 0·0	—	2	1	1·7
Waterhead Bay (3)	W	*h–g*		8	31	52	1·5
			Sigara falleni				
Duck Tarn (1)	NL	*o–n*	3·5 and 3·0	13	—	—	3·0
Duck Tarn (4)	NL	*o–n*		3	—	—	3·0
Pull Wyke Swan	NL	*n–m*		6	2	—	2·75
Pull Wyke Swan (2)	NL	*n–m*	3·0 and 2·5	2	1	—	2·7
Pull Wyke Stream	NL	*n–m*		20	12	—	2·7
Duck Tarn (3)	NL	*m–l*	2·5 and 2·0	4	2	—	2·7
Wise Een Tarn (4)	NL	*m–l*		—	2	—	2·0
*Bank Hey (3), Blackburn	SL	*l–k*	2·0 and 1·5	—	3	—	2·0
*Bank Hey (2), Blackburn	SL	*l–k*		3	5	—	2·4
Pull Wyke Stream (3)	NL	*k–i*	1·5 and 1·0	7	36	8	2·0
Brathay Bar (3)	W	*k–i*		11	12	—	2·5
Waterhead Bay (1)	W	*i–h*	1·0 and 0·5	—	1	—	2·0
White Cross Creek (2)	W	*h–g*	0·5 and 0·0	—	1	1	1·5
			Corixa affinis				
*Kingsmere (1)	S	*i–h*	1·0 and 0·5	—	1	10	—
Kingsmere (2)	S	*h–g*	0·5 and 0·0	—	—	8	—
*Roehampton Pond	S	*h–g*		—	2	15	—
			Sigara limitata				
*Kingsmere (1)	S	*i–h*	1·0 and 0·5	—	2	3	—
*Kingsmere (2)	S	*h–g*	0·5 and 0·0	—	1	7	—
			Sigara distincta				
Slew Tarn (5)	NL	*o–n*		8	1	1	2·7
Clay Pond (3)	NL	*o–n*		6	1	—	2·9
Barngates Quarry	NL	*o–n*		1	—	—	3·0
Slew Tarn (3)	NL	*o–n*	3·5 and 3·0	3	1	—	2·75
Congo Mouth (2)	NL	*o–n*		25	2	—	2·9
Congo Mouth (3)	NL	*o–n*		4	1	—	2·8
Duck Tarn	NL	*o–n*		22	—	—	3·0
Pull Wyke Stream	NL	*n–m*		5	13	2	2·1
Pull Wyke Stream (2)	NL	*n–m*		6	5	—	2·5
Pull Wyke Swan	NL	*n–m*		2	1	—	2·0
Pull Wyke Swan (2)	NL	*n–m*	3·0 and 2·5	2	—	—	3·0
Congo Mouth (1)	NL	*n–m*		22	8	—	2·7
Duck Tarn (2)	NL	*n–m*		17	1	—	2·9

Habitat		Colour of habitat: Between standards	Colour of habitat: Between values	Colour of insects: o–m	Colour of insects: m–k	Colour of insects: k–h	Av. colour of insects
			Sigara distincta				
Barngates Quarry (2)	NL	m–l		1	—	1	2·0
Wise Een Tarn (4)	NL	m–l		1	3	—	2·0
Clay Pond	NL	m–l		1	7	4	1·75
Duck Tarn (3)	NL	m–l	2·5 and 2·0	48	17	—	2·75
Slew Tarn (6)	NL	m–l		2	2	—	2·5
Slew Tarn (7)	NL	m–l		20	14	—	2·6
White Cross Creek	W	m–l		3	2	—	2·0
Wise Een Tarn (5)	NL	l–k		—	2	1	1·7
Cherry Tree Quarry (4)	SL	l–k	2·0 and 1·5	4	9	10	1·7
Bank Hey (2)	SL	l–k		4	7	—	2·35
New Tarn	W	k–i		6	21	12	1·8
Barngates Quarry (4)	NL	k–i	1·5 and 1·0	3	2	—	2·6
Pull Wyke Stream	NL	k–i		3	7	1	2·2
Wise Een Tarn (6)	NL	k–i		2	11	2	2·0
White Cross Creek (2)	W	h–g	0·5 and 0·0	—	1	3	1·25
Wise Een Tarn (7)	NL	h–g		—	—	1	1·0
			Sigara scotti				
Wise Een Tarn (8)	NL	o–n		60	11	—	2·85
Congo Mouth (3)	NL	o–n	3·5 and 3·0	5	—	—	3·0
Brathay Bay (3)	W	o–n		5	1	—	2·8
Blelham Tarn	NL	o–n		5	—	—	3·0
Wray Mires Fish Pond (1)	NL	n–m		11	3	—	2·8
Wray Mires Fish Pond (2)	NL	n–m		2	2	—	2·5
Duck Tarn (2)	NL	n–m	3·0 and 2·5	3	1	—	2·75
Pull Wyke Stream	NL	n–m		1	3	—	2·25
Wray Mires (2)	NL	n–m		4	2	1	2·43
Wray Mires Fish Pond (3)	NL	n–m		6	1	—	2·9
Robinson's Tarn (2)	NL	m–l		11	3	—	2·8
Slew Tarn (6)	NL	m–l		2	1	—	2·7
Clay Pond	NL	m–l	2·5 and 2·0	5	1	—	2·8
Duck Tarn (3)	NL	m–l		5	6	—	2·45
Wise Een Tarn (4)	NL	m–l		31	29	—	2·0
Wise Een Tarn (5)	NL	l–k		17	30	17	2·0
Wise Een Tarn (9)	NL	l–k		22	36	1	2·35
Brathay Bay	W	l–k	2·0 and 1·5	4	22	16	1·7
Wray Mires (4)	NL	l–k		2	4	—	2·3
Barngates Quarry (3)	NL	l–k		2	—	—	3·0
New Tarn	W	k–i	1·5 and 1·0	2	17	5	1·9
Barngates Quarry (4)	NL	k–i		—	1	1	1·5
Wise Een Tarn (10)	NL	i–h	1·0 and 0·5	3	8	6	1·8
			Sigara fossarum				
Wise Een Tarn (8)	NL	o–n		15	3	—	2·8
Blelham Tarn	NL	o–n	3·5 and 3·0	5	1	—	2·8
Clay Pond (3)	NL	o–n		8	—	—	3·0
Slew Tarn (3)	NL	o–n		5	1	—	2·8
Congo Mouth (1)	W	n–m		25	4	—	2·8
Congo Mouth (4)	W	n–m		11	1	—	2·9
Duck Tarn (2)	NL	n–m		2	—	—	3·0
Wray Mires Fish Pond (2)	NL	n–m		3	2	—	2·6
Wray Mires Fish Pond (3)	NL	n–m	3·0 and 2·5	2	—	—	3·0
Blelham Tarn (2)	NL	n–m		5	1	—	2·8
Wray Mires (2)	NL	n–m		6	—	—	3·0
Pull Wyke Stream	NL	n–m		3	—	—	3·0
Wise Een Tarn (4)	NL	m–l		17	5	—	2·8
Clay Pond	NL	m–l	2·5 and 2·0	35	22	7	2·5
Lost Tarn	NL	m–l		4	5	—	2·5
Wise Een Tarn (5)	NL	l–k		5	9	—	2·4
Wise Een Tarn (9)	NL	l–k	2·0 and 1·5	3	18	1	2·0
Brathay Bar	W	l–k		—	2	1	1·7
Wise Een Tarn (10)	NL	i–h	1·0 and 0·5	2	3	1	2·2
Wise Een Tarn (7)	NL	h–g	0·5 and 0·0	2	3	4	1·5

Habitat		Colour of habitat: Between standards	Colour of habitat: Between values	Colour of insects: *o–m*	Colour of insects: *m–k*	Colour of insects: *k–h*		Av. colour of insects
			Sigara nigrolineata					
				o–m	*m–k*	*k–h*	*h–e*	
*Peat Pool (1)	W	*o–n*	3·5 and 3·0	8	1	—	—	2·9
*Peat Pool (2)	W	*o–n*		6	3	—	—	2·7
*Peat Pool (3)	W	*o–n*		3	—	—	—	3·0
*Peat Pool (4)	C	*o–n*		2	—	—	—	3·0
Wise Een Tarn (1)	NL	*n–m*	3·0 and 2·5	1	—	—	—	3·0
*Peat Pool (5)	W	*n–m*		3	3	—	—	2·5
Duck Tarn (3)	NL	*m–l*	2·5 and 2·0	1	8	—	—	2·1
*Peat Pool (6)	C	*m–l*		8	—	—	—	3·0
*Wilpshire Quarry (1)	SL	*m–l*		2	5	2	—	2·0
*Lammack Pool	SL	*i–h*	1·0 and 0·5	3	30	25	—	1·6
*Ornamental pond, Blackburn	SL	*h–g*	0·5 and 0·0	—	2	4	—	1·3
*Dene Ground, Hawkshead	NL	*f–e*	−0·5 and −1·0		9	52	3	1·1
			Cymatia bonsdorffi					
Slew Tarn (3)	NL	*o–n*	3·5 and 3·0	5	—	—		3·0
Slew Tarn (7)	NL	*n–m*	3·0 and 2·5	1	3	—		2·25
Little Ludderburn Tarn	W	*n–m*		9	2	—		2·8
Rather Heath	W	*m–l*	2·5 and 2·0	3	17	—		2·1
Lost Tarn	NL	*m–l*		—	1	—		2·0
New Tarn (2)	W	*m–l*		3	1	—		2·75
Podnet Tarn	W	*m–l*		2	1	—		2·7
New Tarn	W	*k–i*	1·5 and 1·0	—	4	1		1·8
			Sigara wollastoni					
*Peat Pool (1)	W	*o–n*	3·5 and 3·0	2	—	—		3·0
*Peat Pool (2)	W	*o–n*		7	2	—		2·8
*Peat Pool (3)	W	*o–n*		1	—	—		3·0
*Peat Pool (4)	C	*o–n*		5	1	—		2·9
*Peat Pool (5)	W	*o–n*		4	1	—		2·8
*Peat Pool (6)	C	*o–n*		7	1	—		2·9
*Peat Pool (7)	W	*n–m*	3·0 and 2·5	2	2	—		2·5
*Peat Pool (8)	W	*n–m*		—	4	5		1·5
*Peat Pool (9)	W	*l–k*	2·0 and 1·5	—	3	3		1·5
*Wilpshire Quarry (2)	SL	*l–k*		10	53	48		1·6
*Peat Pool (10)	W	*k–i*	1·5 and 1·0	—	2	3		1·4
			Micronecta poweri					
				m–k	*k–h*	*h–f*		
High Wray Bay	NL	*l–k*	2·0 and 1·5	6	2	—		1·75
Waterhead Bay	W	*l–k*		8	1	—		1·9
Brathay Bar	W	*l–k*		2	3	—		1·4
Boathouse (3) (*a*)	NL	*k–i*	1·5 and 1·0	2	22	4		1·0
Boathouse (3) (*b*)	NL	*k–i*		2	15	3		1·0
High Wray Bay (2)	NL	*i–h*	1·0 and 0·5	1	3	4		0·6
Pull Wyke Stream (4)	NL	*i–h*		—	5	7		0·4
Brathay Bar (4)	NL	*h–g*	0·5 and 0·0	5	20	6		1·0
High Wray Bay (3)	NL	*h–g*		1	3	4		0·6
Sandy Wyke	NL	*g–f*	0·0 and −0·5	—	4	—		1·0
Sandy Wyke (2)	NL	*f–e*	−0·5 and −1·0	—	1	8		0·1
Waterhead Bay (4)	W	*f–e*		—	1	9		0·1

STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

X. PROLONGED LARVAL LIFE AND DELAYED SUBSEQUENT EMERGENCE OF THE ADULT GALL MIDGE

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1. INTRODUCTION

In the fourth (1) and fifth (2) of these studies evidence was brought forward concerning prolonged larval life and the resultant delayed emergence of the adults in two multi-voltine gall midges, *Dasyneura alpestris* (Kieffer) (*D. arabis* Barnes) and *D. pyri* (Bouché). It was shown that, although 100% of the larvae of the first generation in the year always developed into adult midges the same year, varying proportions of the second, third and fourth generations had in some seasons a prolonged larval existence and did not complete their life cycle until the following year. As a consequence the first flight of a year is at times made up of varying numbers of the G_2, G_3 and G_4 of the previous year. For example, as much as 7% of the second generation, 52% of the third generation and 100% of the fourth generation of 1932 did not emerge as adult midges until 1933. In other seasons, e.g. 1929, 100% of the first and second generations and 84% of the third emerged the same year, leaving only all the fourth generation and 16% of the third generation to overwinter as larvae. Both these examples refer to *D. pyri.*

In the eighth (3) of this series the same type of delayed emergence was noted in two uni-voltine gall midges, *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Géhin). Evidence was then given that the larvae of *Contarinia tritici* could spend two winters in the soil before emergence of the adults took place and that those of *Sitodiplosis mosellana* could spend three.

The object of the present paper is to give more evidence of this prolonged larval life and subsequent delayed emergence of the adult wheat blossom midges, *Contarinia tritici* and *Sitodiplosis mosellana.*

Flexibility in the duration of the larval stage is both an insurance against the sudden obliteration of a species (e.g. by untoward weather conditions) and a possible cause and explanation of sudden increases in insect numbers.

Each year the larvae of the wheat blossom midges have been placed in breeding cages soon after their abstraction from the wheat ears in the course of ascertaining the infestation of the wheat crop on Broadbalk field. Since 1939 these cages have been retained and the numbers of midges emerging each year have been noted. The following remarks apply to midges reared under insectary conditions, not out in the field. It is thought that what has happened so regularly under these conditions might equally apply under field conditions in some years.

2. *CONTARINIA TRITICI*

It was previously shown (3) that a single female of this, the lemon-coloured wheat-blossom midge, emerged in the spring of 1940 from a larva abstracted from a wheat ear not later than the summer of 1938. The deduction was that the larvae of this species could survive two winters in the soil.

It was also shown that a partial emergence of this species took place in the August or September (in 11 years out of 13) of the same year as the larvae occurred in the wheat ears.

Table 1 gives the numbers of *C. tritici* and its parasites* that have emerged from larvae collected in the summers of 1939, 1940, 1941 and 1942 and the year in which such emergences have taken place.

Table 1. *Emergence of* Contarinia tritici *and its parasites*

Larvae collected in	Numbers of *C. tritici* and its parasites which emerged in 1939	1940	1941	1942	1943
1939	Some	588–1	0–0	0–0	0–0
1940	—	2–0	335–159	32–3	0–0
1941	—	—	0–0	131–38	1–0
1942	—	—	—	4–0	295–87

First of all it can be seen that in three out of four years there was a slight emergence the same year (in late August) as the larvae were collected. Secondly, in each case most of the emergences both of host midge and its parasites took place the year after the larvae had been collected. Thirdly, quite a few (32 or 4%) of the larvae collected in 1940 did not produce midges until 1942 and one larva collected in 1941 developed into a midge in 1943. This is further evidence that the larvae of this species can spend two winters in the soil after leaving the wheat ears. Fourthly, no midges have up to the present developed later than during the second summer after the larvae have been on the wheat.

As regards the parasites of this midge, none have been observed to develop into adults later in the

* These and the parasites of *Sitodiplosis mosellana* have not yet been identified.

same year as the midge larvae were collected, but in one year (1942) three parasites emerged from larvae which had been collected in 1940.

3. *SITODIPLOSIS MOSELLANA*

It was previously shown (3) that the spending of two winters in the soil in the larval stage by this, the orange-coloured wheat-blossom midge, was of more frequent occurrence than in the case of *Contarinia tritici*. In fact five *mosellana* were recorded as spending three winters in the soil before emergence as adult midges.

Table 2 gives the numbers of *Sitodiplosis mosellana* and its parasites that have emerged from larvae collected in the summers of 1939, 1940, 1941 and 1942 and the year in which such emergences have taken place.

Table 2. *Emergence of* Sitodiplosis mosellana *and its parasites*

Larvae collected in	Numbers of *S. mosellana* and its parasites which emerged in			
	1940	1941	1942	1943
1939	192–68	44–0	44–0	100–0
1940	—	543–412	236–91	79–0
1941	—	—	516–468	139–76
1942	—	—	—	281–337

No *S. mosellana* have been known to reach the adult midge stage the same year as the larvae have been attacking the wheat ears. As if to compensate for this some of the larvae in each year's material have remained in the soil as larvae for more than one winter. In fact, up to the present midges have emerged each ensuing year from material collected in 1939, 1940, 1941 and 1942. Thus in the case of the larvae collected in 1939, 192 midges emerged in 1940, 44 in 1941, 44 in 1942 and 100 in 1943. This is definite proof that the development of the adult midge can be delayed until two, three, and even four winters have lapsed since the larvae were in the wheat ears. Only future observation will show whether four winters in the soil is the maximum period or not.

The numbers of midges which have emerged after two, three or four winters are considerable. Thus considering the numbers of larvae originally put in the breeding cages, 2·7, 14 and 7·9 % have emerged after two winters, 2·7 and 3·4 % after three winters and 6·2 % after four winters. These figures must be considered in relation to those of the percentage emergences after only one winter in the soil, i.e. 16, 42, 36 and 30. The possibility of such retarded development being a cause or explanation of sudden increases in midge numbers is emphasized when one considers the origin of the adult midges emerging in any one year. Thus, of the midges emerging in 1943 roughly 47 % were derived from larvae of the previous year (1942), 23 % were derived from two years previously (1941), 13 % from three years previously (1940) and 17 % from four years previously (1939).

Turning to this midge's parasites it will be seen (Table 2) that quite a number have similarly not appeared as adults until two winters have lapsed. For example, 91 parasites emerged in 1942 from the 1940 material and 76 in 1943 from 1941 material. So far no parasites have remained dormant for longer than this.

4. SUMMARY

1. The emergence of *Contarinia tritici* adults can occur in the autumn of the same year as the larvae attack the wheat, during the next spring and after a lapse of two winters. Its parasites generally emerge after the first winter but have been known not to emerge until after the second.
2. The emergence of *Sitodiplosis mosellana* takes place up to four years after the larvae have attacked the wheat, but not later in the same year. Its parasites can survive two winters in the soil.
3. The effect of this variability in the duration of the larval stage in preserving the race and as a cause of sudden increases in numbers is pointed out.

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THE NATURAL HISTORY OF THE MINNOW, *PHOXINUS PHOXINUS*

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(With 9 Figures in the Text)

CONTENTS

1. INTRODUCTION

The minnow, *Phoxinus phoxinus* (L.), is found in most of Europe except the Mediterranean littoral region and in Siberia; it also occurs in the Crimea (Berg, 1932). Records and observations indicate that it is fairly generally distributed in the British Isles, ranging 'north to the R. Deveron' but being 'absent from the Northern Highlands of Scotland' (Regan, 1911); its distribution in Ireland is not so restricted as was once supposed.

The minnow inhabits flowing waters, ponds, shallow lakes and the fringes of deep lakes. It may be found where there is silt and vegetation, but a preference is shown for a bottom of stones and gravel. In lakes it usually occurs where the wave action is moderate and in rivers where the current is gentle. It frequents waters of a wide range in altitude; in the Lake District it has been recorded from Sprinkling Tarn, 1960 ft. (Watson, 1925) and observed in Grisedale Tarn (Helvellyn), 1768 ft. In Windermere it tolerates ice-covered waters and a temperature of 23° C.; on the Continent it has been taken where the temperature was as high as 31° C. Records from which to deduce the minnow's tolerance of chemical conditions are scanty, but it certainly lives in great numbers in the soft acid waters of Grisedale Tarn in the Lake District, and it is also abundant in the chalky waters of the south of England. In Ireland, also, the minnow has been observed to be common in both acid and alkaline waters, the enormous numbers noted in the latter refuting Day's remark (1880) that in that country they are 'scarce where calcareous rocks predominate'.

Although much general information about the minnow is available in Yarrell (1836), Couch (1865), Day (1880), Regan (1911) and similar books dealing with the fishes of the British Isles, and in Bade (1901–2), Vogt & Hofer (1909), Willer (1924), Thienemann (1911) and Wunder (1936) and other Continental works on fish, no comprehensive work on the natural history of *Phoxinus* had been published until Tack's monograph appeared in 1940. Owing to war conditions this paper did not come to my knowledge until September 1942, by which time my work had been planned and most of it executed. It is interesting that an investigation carried out by two workers, namely, Tack and myself, entirely independently, had been planned on similar lines and gave results which in many cases confirmed each other.

The present investigation deals with the habits, growth, food and reproduction of the minnow from a large lake (Windermere) and a trout stream (River Brathay): the feeding habits of some trout fry from the river were investigated for comparison with those of the minnow. The material was obtained between December 1939 and May 1942.

2. MATERIAL AND METHODS

Windermere has a length of 10·5 miles (17 km.), a mean breadth of 950 yd. (874 m.) and a mean depth of 75 ft. (24 m.); there is a narrow littoral zone. The water of the lake is soft, and has a pH value of about 6·8. The fish to be found in the lake are the eel (*Anguilla anguilla* (L.)), salmon (*Salmo salar* L.), brown trout (*S. trutta* L.), char (*Salvelinus alpinus willughbii* (Günther)), pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), stickleback (*Gasterosteus aculeatus* L.), the bullhead (*Cottus gobio* L.) and the minnow (*Phoxinus phoxinus* (L.)). The minnow inhabits the littoral zone, frequenting water from about 6 in. to 12 ft. in depth. The specimens examined for this investigation were taken from shallow water where the bottom was of stones and gravel.

The River Brathay, which is one of the major inflows into Windermere, is a quickly flowing trout stream, the chemical character of its waters being much like that of Windermere. In addition to the minnow, the brown trout, stickleback, stone loach

(*Nemachilus barbatula* (L.)) and bullhead are present. The minnows usually live in water of about 4 in. to 2 ft. in depth in the more slowly flowing parts of the river, and the samples were taken from such a reach three-quarters of a mile from the river's outflow into the lake.

Collection

The capture of minnows from Windermere began in December 1939 and from the River Brathay in May 1940; two collections each month were made from each of these environments during two years following these dates. The method of collection of the material depended on the habitat of the minnow which is conditioned by the season (p. 143).

The lake material was obtained:

(*a*) From April to October, when the minnows are active and swimming in shoals in shallow water, by a $\frac{1}{4}$ in. mesh seine worked either from a boat or the shore.

(*b*) From November to early April, when the minnows are quiescent and hiding under stones, by means of 'trays'.* These trays are essentially the same as those described by Moon (1935) and used by him to collect the lake-bottom fauna. Each tray consisted of a strong iron frame measuring a yard square, to which a square of canvas (previously treated in Cuprinol to prevent rotting) had been sewn; this shallow canvas bag was supported by a square of 3 in. wire netting fastened on the frame. Bridles were attached to each of the corners of the frame and they passed into a lowering rope. The trays were covered with stones so as to resemble the lake bottom and set at stations where minnows had been seen in the summer-time; two such stations were chosen for the winter of 1939–40, to which a third was added in that of 1940–1. During the first winter a tray was set at 1, 2, 3 and 4 m. depth at each station, but since the majority of the fish were taken between 1 and 2 m. the trays were put down at $\frac{1}{2}$, 1, $1\frac{1}{2}$, 2 and 3 m. throughout the following winter. The trays were raised periodically each month to collect the fish.

The river material was obtained:

(*a*) From April to November by seine.

(*b*) From November to March by lifting up stones near the water's edge and then capturing by hand or hand net the minnows found under them.

By these methods some 2600 minnows from Windermere and over 1800 from the River Brathay were obtained for examination.

Measurements

The fish were measured from the tip of the snout to the fork of the caudal fin. In some collections, and for all fish examined for gut contents and age determinations, the individual length to the nearest millimetre was taken; for large collections the measurements were made to the nearest 0·5 cm. The minnows taken during the two years' routine collections, arranged in half-centimetre length groups, are given in Table 1. These figures will not give an accurate picture of the relative proportions of the different length groups in the lake and river, since the size of the seine mesh and the personal factor affected the capture of the fish. The marked falling off in the numbers and percentage proportion of minnows of over 60 mm. in both environments is, however, probably true for natural conditions, since such larger fish are least likely to escape through the net.

During the first year the members of any one 5 mm. length group were weighed in bulk and the average weight of each fish obtained from this weighing. Individual weights of some fish examined for age or food were taken throughout the investigation.

The sex and condition of the gonad was noted for many fish examined (p. 157).

Age determinations

These were based on otoliths, scales and length-frequency distributions (p. 144). Bullough (1940) when studying sex reversal in the minnow determined the age of his specimens from their otoliths. In view of this these very small (0·6–1·05 mm. long) spherical bodies were examined; good specimens show alternating milky white and dark transparent bands when seen by reflected light. These were interpreted as indicating summer and winter growth respectively. Scales taken off the shoulder of the minnow, as in salmonid fishes, were examined. The circuli on such scales appeared to be more or less evenly spaced and thus allowed of no interpretation in terms of growth periods. Tack (1940) took scales from above the lateral line in the caudal peduncle region and found that these have a number of widely spaced more or less concentric circuli followed by a group of narrowly spaced irregular ones; the former represent the summer growth, the latter that of the winter (Fig. 3). Radial lines, a new series of which is laid down with each summer zone, may further indicate the annual growth areas. Tack corroborated his age determinations from scale reading by those he obtained from the interpretation of length-frequency curves. His method of scale reading has been used in the present study. Scale readings of Windermere and Brathay fish were supplemented by analysis of records for length-frequency distribution.

Gut examinations

The gut contents of 1228 minnows from Windermere and 833 from the River Brathay were examined and the results tabulated. The gut of the minnow from mouth to vent was examined for food. The

* This method of collecting minnows in winter time was suggested to me by the fact that when Moon was investigating the invertebrate fauna of Windermere he found that, during the winter, numbers of minnows had hidden amongst the stones on trays which he had set in the lake to be colonized by the invertebrates.

animal food organisms were counted individually, or if large numbers were present a rough visual estimation of their numbers was made. For algae, diatoms and other vegetable matter, the extent to which they filled the gut was noted. Some of the animal food organisms were identified to species, others only to the genus or group. Specimens of the most frequently occurring diatoms and filamentous algae were determined. The plants and animals were classified into significant food groups, which are arranged in the tables in order of their forming surface, mid-water or bottom feeding for the minnow, abundance, the size of the individual organisms as well as their abundance being taken into account. It will be realized that this evaluation is essentially an estimate of bulk and that the points represent absolute values and not relative ones; therefore the degree of fullness of the gut was also taken into account when assessing points. The following examples will explain how the method works: The gut of one fish is full and contains twelve nymphal Ephemeroptera, six larval Trichoptera and fifty Cladocera; the Ephemeroptera occupy most of the room and are given 3 points, the Trichoptera bulk

Table 1. *Total minnows captured, divided into 5 mm. length groups*

Length group	10·5–	15·5–	20·5–	25·5–	30·5–	35·5–	40·5–	45·5–	50·5–	55·5–	60·5–	65·5–	70·5–	Total
							Windermere							
Jan.	—	—	3	17	17	6	13	15	8	3	—	—	—	82
Feb.	—	1	8	28	13	6	6	11	6	2	—	—	—	81
Mar.	—	—	11	14	16	9	7	13	3	2	1	—	—	76
Apr.	—	1	28	52	66	17	23	39	18	12	10	7	—	273
May	—	8	97	181	101	25	49	65	51	19	11	—	—	607
June	—	—	5	16	19	21	29	16	11	10	4	3	—	134
July	2	13	8	—	4	12	46	68	88	41	22	10	2	316
Aug.	—	5	35	14	1	14	48	95	71	18	18	5	—	324
Sept.	—	47	75	32	2	4	15	77	95	35	21	3	1	407
Oct.	—	—	4	24	13	13	27	66	62	36	5	2	—	252
Nov.	—	1	—	4	1	—	2	—	—	—	—	—	—	8
Dec.	—	—	2	25	8	1	7	9	5	13	4	1	—	75
Total fish	2	76	276	407	261	128	272	474	418	191	96	31	3	2635
% prop. diff. length groups	—	2·9	10·5	15·5	10·0	4·9	10·3	18·0	15·9	7·3	3·6	1·1	—	100·0
							River Brathay							
Jan.	—	—	—	1	—	1	2	1	4	6	2	1	—	18
Feb.	—	—	—	—	—	2	4	1	5	—	1	1	—	14
Mar.	—	—	—	—	1	—	5	3	4	5	2	2	—	22
Apr.	—	—	—	—	—	—	7	18	15	11	16	2	—	69
May	—	—	—	8	27	35	45	64	48	23	11	—	1	262
June	—	—	—	16	90	55	49	50	34	10	4	—	—	308
July	—	—	—	—	7	43	130	215	72	23	5	—	1	496
Aug.	13	16	20	2	1	26	58	61	21	12	6	—	—	236
Sept.	—	—	—	—	2	5	26	35	40	32	9	1	—	150
Oct.	—	—	1	9	4	15	30	52	57	29	7	2	—	206
Nov.	—	—	—	1	—	2	1	2	3	1	1	—	—	11
Dec.	—	—	—	—	—	—	2	5	7	1	5	—	—	20
Total fish	13	16	21	37	132	184	359	507	310	153	69	9	2	1812
% prop. diff. length groups	0·7	0·8	1·2	2·1	7·3	10·0	19·8	28·0	17·3	8·5	3·8	0·5	—	100·0

the first two groups being of the first type, the next four of the second and the remainder may be regarded as bottom food.

In evaluating the different food organisms the method of Swynnerton & Worthington (1940) has been adopted, with modifications, since it has the advantage of giving roughly quantitative as well as qualitative data without the need for detailed counts or weighings. The contents of the gut of each fish were identified and the organisms of each food category either counted or their masses assessed by eye. Each category represented was then given a number of points—3, 2, or 1—according to its less and are given 2 points, and the Cladocera (although greater in number) have about the same bulk as the Trichoptera and are also given 2 points, the total for the gut thus amounting to 7. The gut of another fish contains the same food in the same proportions but is half empty; the Ephemeroptera are evaluated at 2 points and the Trichoptera and Cladocera at 1 point each, the total for this gut being only 4.

In summarizing the data, the total number of integers for each separate food group was found for each of the 10 mm. length groups into which the minnows had been divided, and by adding the results

from the different length groups together the total integers for each food category was obtained. The totals obtained are scaled down to a percentage basis in the tables.

Other fish examined

During the investigation fifty trout fry were caught in the River Brathay in April, May, June, July, August, September and December, and their stomach contents examined in order that their food might be compared with that of the minnows from the same locality (p. 157). No fish of any species for such comparative purposes were taken from Windermere.

3. RESULTS

(*a*) *External features*

The minnow is one of the smallest British freshwater fishes. The largest specimen taken during the present work measured 82 mm. (3·3 in.) and weighed 6·6 g. Specimens of 80 mm. were not often found, the general run of adult fish being from 50 to 65 mm. long. It is alleged that big minnows occur in the high tarns of the Lake District, and Day (1880) mentions that specimens 7 in. long were taken from a stream running into Wastwater. Minnows investigated by Tack from waters in western Germany were as much as 119 mm. in length.

The external features of *Phoxinus* vary but little with the individual fish, but some of them are affected by age and sexual conditions. The scales, which are small (large ones are only about 0·9 mm. long), cover the body except for an area of variable extent on the belly between the pelvic and pectoral fins. Bade (1901–2) says that they are also absent from places on the back, but I found no such bare patches. Scales first appear when the fish is about 16 mm. long, when it would be approximately 5 months old.

The colouring of the adult minnow, except in the breeding season, is as follows: the back and the sides in the region of the lateral line have a background colour of dark olive brown, overcast on the flanks with a golden or copper bronze iridescence. The ventral surface is yellowy white with a silver sheen. A thin golden stripe runs down the side, a little above the lateral line, from the operculum to the tail. There is a series of vertical black stripes down the sides. The top of the head is dark olive brown and the opercula are bronzed. The paired fins are golden brown and the dorsal, anal and caudal fins are dark in colour.

Young sexually immature minnows (*c.* 25–35 mm.) have the dark colouring and stripes on the back, which has an almost mauve bronze sheen over it; the golden iridescence of the sides is missing, and the belly is silver white. These young fish have a black line running down the side from head to tail, a feature which is absent in bigger fish, and Tack (1940) indicates that this line is replaced by the vertical stripes in the older and sexually mature specimens.

The characteristics described above apply to both sexes. I have found no evidence to support Bullough's remark (1940) that 'The sexes may be distinguished externally by the light coloration of the female and by the dark pigmentation of the male.' Distinctive colouring, and also characters are, however, found in both male and female at breeding time, as described below; but at all times the sexes may be distinguished by certain morphological characteristics. These have been studied by Tack from a wealth of morphometric data and by Bade (1901–2) and Vladykov (1927) to a lesser extent. It was not thought necessary in the present investigation to collect such material, but the German workers' conclusions are reviewed and the salient points given here.

Tack noted that the difference in length of male and female fish in their first, second and third years was inconsiderable, but in the following year classes the male was appreciably smaller than the female. In Windermere the difference in length between males and females in their first and second year is insignificant, but the three-year-old males are much smaller than the females (p. 147).

Tack and Vladykov both measured and compared the length of the pectoral fin of male and female fish and concluded that the male had the longer fin. Tack maintains that the distinction is applicable to both immature and mature minnows, although it may not be so marked in three- and four-year-old fish. He concludes that the distinction cannot, however, be regarded as an infallible one, since considerable overlap of the length variations is possible. No measurements of the pectoral fins of Windermere fish were made, but general examination of some specimens gave the impression that in two- and three-year-old mature individuals the male had a longer fin than the female.

Vladykov (1927) pointed out further differences between male and female fish based on the pectoral fins. He noted that in the male the fin is broad and rounded, i.e. fan-shaped, whereas in the female it is narrow and weakly rounded; Vladykov's specimens would all appear to have been mature fish. In Windermere sexually mature fish show this sexual difference well (Fig. 1), but in immature minnows the pectoral fins have the same shape in both sexes. He observed also that the first eight fin rays of the pectoral fin are thickened in the male and not in the female, a character which first appears in sexually ripe individuals and remains for the rest of the life. Windermere fish showed this sexual dimorphic character well at breeding time, but outside this period it was a little less obvious; no thickening of the fin rays was seen in immature fish.

The foregoing account of the colour and of the sexual dimorphic characters of the minnow may be concluded by an account of these characteristics in

breeding fish. It is based on specimens taken from a spawning shoal in the River Brathay on 3 May 1942; the fish were described on the spot. In the male the back was a green-black, the sides a metallic emerald green with vertical dark stripes; the ventral surface from the proximal end of the jaw to the caudal fin was an intense scarlet. The head was bronze green; under the throat was matt black and the upper and lower jaws had a touch of scarlet. The paired and anal fins were slightly tinted with scarlet, and on the base of these fins there was a milk-white spot, the edge of the opercula also showing a similar white colouring. When the minnows were swimming

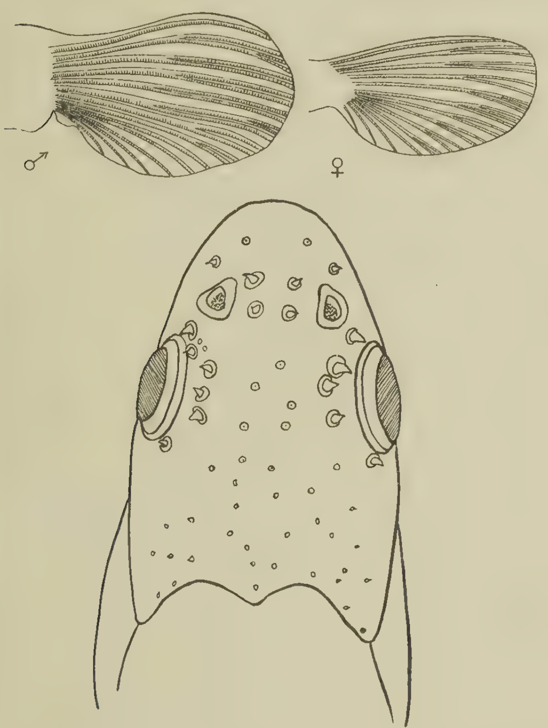

Fig. 1. Head of male minnow at breeding time and pectoral fins of sexually mature male and female fish.

these white marks gave a flecked flutter to the dark mass of fish. On the top of the head were a number of milk-white spinose tubercles which have the arrangement shown in Fig. 1.

The female had much the same colouring of back and sides as the male, the metallic sheen of the sides being perhaps more golden and less green than the male. The red of the ventral surface was not so intensely scarlet as in the male and did not extend the full length of the body, since there was a whitish area which began in the pelvic region and extended forwards for about half the abdominal length. The fins and opercula had the same colouring as in the male. The head tubercles were also present although, in some specimens, much less boldly developed.

The breeding coloration in the male is weakly suggested as early as mid-March, but neither male nor female have head tubercles at this time. In both sexes the tubercles are lost after spawning and a tiny hole on the head marks their place. In the spent condition the female may show some small trace of the red colouring on belly and fins or may lose all of the distinctive breeding coloration, whereas the male retains more definite traces of the red colour and may also have the white marks on fins and opercula. Immature fish of both sexes have none of the reproductive colours nor have they the head tubercles.

Vladykov notes that there are epithelial papillae on the pectoral fins of the males in the spawning season. These are of two types: (1) on the upper surface of the fin there are tiny pointed papillae set in two or three rows on the first seven thickened fin rays, (2) on the upper and under surface of the fin are other minute papillae, seldom arranged in rows, and situated on the skin between the fin rays. Examination of breeding males from Windermere and the River Brathay showed that both types of papillae were present, but it was noted that in some cases the first type were found on both upper and under surfaces of the fins and that they might also be present on the 8th thickened fin ray; when present on the under surface the papillae were somewhat haphazard in arrangement. The papillae were absent in fish caught in October when all spawning is over. A characteristic of the spawning livery noted by Tack is microscopic white spots on the edge of the scales of the caudal region. Their arrangement and number in both sexes is the same, but those of the male are, however, somewhat larger; they disappear when spawning ends. On examination of breeding fish in the River Brathay similar spots were found.

There seems no doubt but that the breeding dress in its most marked form is associated only with spawning time, a view held by many observers; but Vladykov (1927) points out that in the writings of Siebold, of Hofer and of Bade it is maintained that the breeding coloration is independent of spawning time. Some writers have attributed the head tubercles to the breeding male only, but there is no evidence of this from Windermere minnows.

(b) *Habits and movements*

In Windermere minnows occur on any kind of bottom but with a preference for the stony type; they appear to withstand a fair amount of wave action. In the River Brathay they are found where the river bottom is stony and the current gentle and also in the backwaters where there is much vegetation; only during spawning time have they been noted in swift water. In both lake and river during late spring, summer and autumn minnows are pelagic, frequenting water from 30 to 60 cm. (1–2 ft.) in depth. They live in shoals which may comprise a hundred or more fish of all sizes. Some tendency for segregation into length (age) groups, as shown by the

separation of the fish, although in close proximity, into congregations of small (one-year-old, immature) and larger (two- and three-year-old, mature) individuals, has been observed. Such segregation is much more apparent in spawning and spent fish.

At spawning time the mature lake minnows migrate in large numbers up the inflowing streams, but apart from this no other mass movement has been observed. Bade (1901–2) remarks on the migrations of enormous numbers of minnows from the warmer and lower reaches of the river to the cooler waters upstream during the summer-time.

During the winter the fish are no longer seen in open water but are found, in both lake and river, under stones. In Windermere their habits during this period of retirement were investigated from November to mid-April by means of trays (p. 140). In the River Brathay the use of trays was not feasible, and therefore from November to March the minnow was studied by direct observation on the river. It was found that the lake minnows hid under stones of about 3–4 in. diameter in preference to 1 in. gravel, a habit which was shared by the river fish. Although benthic the minnows maintained their gregarious habit; as many as thirty-four were found on one tray. Those taken ranged in length from 16 mm. (O-year class) to 65 mm. (II-year class). Individuals of all lengths would be found on one tray, although instances of the tray's population being either of small (immature) fish or of large (mature) specimens, suggesting an age class segregation, were found. Minnows colonized the trays set at each depth (p. 140) but throughout the winter occurred in greatest numbers at 1½ and 2 m. This indicates that there is a definite movement of minnows from the shallows inhabited in summer to relatively deeper water, preferably some 2 m. in depth, in winter. The numbers taken each time the trays were lifted were too few to show any periodic changes in the population. A large proportion of the fish both from Windermere and the River Brathay contained food.

The over-wintering just described is no doubt modified by local conditions; minnows have been seen swimming in a quiet backwater of Windermere in early December, and in early March they have been similarly observed in a sluggish stream.

It is not clear what factors account for the winter habits. Allen (1940) has shown that young salmon are found only in deep pools from the end of October to the beginning of April, the water temperature then being below 7° C.; active life is resumed when it rises above this point. In Windermere the temperature in November is about 8° C., but it seems unlikely that it may be compared in effect with Allen's 7° C., since active minnows are found in April when the lake temperature may be appreciably below 8° C. It may be that the seasonal changes in the duration of daily light affect the summer and winter habits of the minnow, for Bullough (1939, 1941) has shown experimentally that the amount of light is to some extent one of the factors controlling sexual development of this fish.

(*c*) *Age and growth*

Otoliths, scales and length measurements were all examined in an attempt to determine the age and growth rate (p. 147). Some 300 otoliths were examined but were found to be difficult to read and interpret; results of a somewhat unsatisfactory nature were obtained from about half of them. Scales were taken in the first instance from the shoulder, but these were found to be useless (p. 140); later it was found that those from the caudal peduncle were of value for age determination (p. 140, cf. Fig. 3). For length measurements the monthly collections of fish from Windermere and the River Brathay for two years were arranged in 5 mm. groups and examined statistically by Mr H. J. Buchanan-Wollaston. He found that, after taking the errors of random sampling into account, data for those months with considerable numbers of fish (e.g. May in Windermere and July in River Brathay) suggested that there were three overlapping length groups with the possibility of a fourth; there was no sign of a fifth. These size groups could reasonably be interpreted in terms of age. Since these samples were not sufficiently large to make the errors of random sampling unimportant it was decided to take a big sample for analysis at one place and time. This was netted from Windermere at the end of April 1942, just before spawning time, when it might be presumed that a new year group had not entered the stock, and again in October towards the end of the same year's growth period. The whole collection from the April netting, 1095 fish, and a sample of 672 from that of October, were divided into 5 mm. length groups, the frequency distribution of which is shown in the graph (Fig. 2). Mr H. J. Buchanan-Wollaston analysed the compound frequency distribution into what he considered to be likely components in each case and these are shown in the figure by a dotted line; his comments on the analysis are as follows:

'Considering the April curve first: the frequency distribution may reasonably be split up into the three normal length distributions shown by the dotted line,* though the theoretical and actual frequencies do not agree exactly, it being justifiably assumed that the discrepancies are due to random sampling errors and to the fact that the spawning season of the minnow is somewhat extended. It is, of course, quite possible to split the complete distribution into more than three components and make the theoretical and actual curves agree exactly, but it is not justifiable to assume that there is no random sampling error. Three age classes are indicated with their

* The curves in Fig. 2 are not normal curves of error but 'area curves' in which any ordinate represents the number of fish in the 5 mm. interval through the centre point of which the ordinate is drawn.

modal sizes at 31·9, 58·6 and 69·9 mm., the O, I and II age groups. The curve for the O-year class has been extended to the left to make it symmetrical; this causes the curve to pass above the points representing the numbers of fish of 27·5 mm. and under. As it is certain that the net allows many of these very small fish to escape it is probable that the theoretical group represents the length frequency of the O class better than the actual sample measured. The length-frequency distribution for October (Fig. 2) appears to comprise only two components, the I and II class,

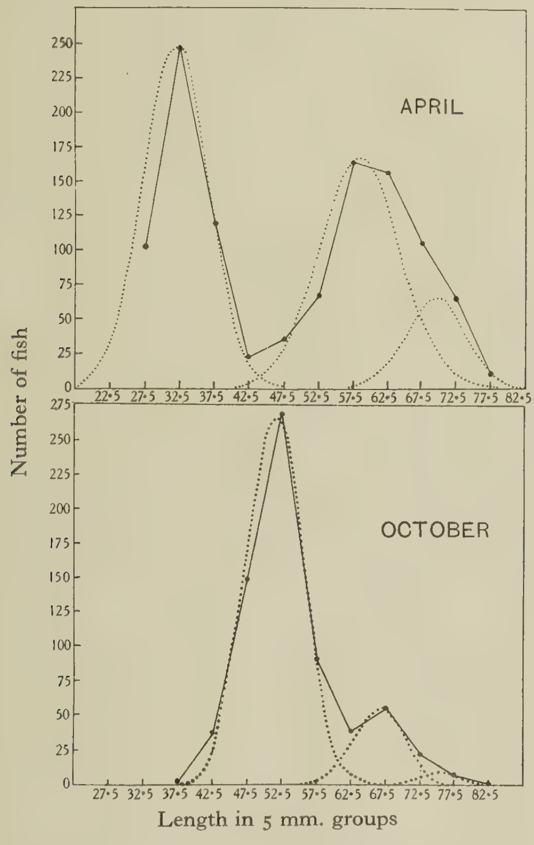

Fig. 2. Length-frequency distribution of Windermere minnows from April and October (1942) hauls. Mr H. J. Buchanan-Wollaston's interpretation shown by the dotted line.

but there is a suggestion certainly of a very small number of the fish belonging to a still older class, since the number of minnows at 72·5 and 77·5 mm. appear to be too great to be all included in the II class.'

The results of this study of the length-frequency distributions threw much doubt on the otolith readings, which in many cases gave the age for any length either one or two years greater than that attributed to it by the frequency curve. When, therefore, in September 1942 I first saw Tack's paper in which he shows that the scales taken from the caudal peduncle above the lateral line are satisfactory for age determination (p. 140), similar scales from Windermere and Brathay fish were examined (Fig. 3).

The Windermere fish were taken from the big haul of April 1942 since, because spawning begins in May, when also the majority of the fish reproduce, a new year group would not be present to complicate the age groupings. The fish were classified as belonging to the O, I and II groups during their first, second and third years of life respectively. The results obtained from reading 286 sets of scales are given in Table 2 and Fig. 4. It was found that a better definition of summer and winter bands was obtained when the scale was slightly stained with methylene blue. Nothing comparable to the spawning mark of the Salmonids was found. The greatest length increase, 49 % of the total average length obtained, is achieved in the first year; the increase of 22·5 mm. in the second year represents about 33 % of the total growth; in the third year an increase of 12·5 mm. only is made, showing the falling off in growth with age increase which characterizes most fish growth rates. Mr Buchanan-Wollaston's analysis of the length-frequency curves of Windermere indicated three year classes, and it will be seen that their modal sizes agree quite well with those found by the scale readings. The likelihood of fish in their fourth year (III group) suggested by the October curve (Fig. 2) has been supported by scales which show 3+ years' growth taken from seven female fish, ranging in length from 73 to 82 mm., which occurred in a haul made in November 1942. Their growth is indicated in Fig. 4 by the broken line which has been extended, since growth has practically ceased by November, almost to the end of the fourth year.

The age of Brathay minnows has been determined from scales only. The fish examined were from spring collections (i.e. those made prior to spawning time) which unfortunately contained relatively few one- and three-year-old specimens. Three year classes were present: the mean length of each is not significantly different from that of Windermere fish, and the length increments maintain the same sequence. Although in the two years' collections no minnows showing 3+ years' growth, such as occurred in Windermere, were captured, three-year-old individuals of 74 mm. in the late May samples suggest that such older fish are not unlikely. (Table 3).

Tack examined the scales of 572 minnows, from four streams, and obtained the following mean values for length (in mm.) attained by the different age groups (the number of fish is given in brackets): O, 34·29 (162); I, 53·12 (221); II, 69·39 (106); III, 85·33 (62); IV, 95·56 (18); V, 113·83 (3). He found no real difference between the length of males and females of the I and II class, but the females of III and IV were much larger than the males. The growth of his O, I and II group fish is much like that for Windermere and the River Brathay. He found,

however, appreciable numbers of minnows in the III group and even some specimens belonging to a IV and V group. In view of this the limitation of life of Windermere and Brathay individuals to 3 or 3+ years is of much interest. If in the length-frequency curve (Fig. 2) more than one year class had been present in the lengths interpreted as II group, it nows would be open to attack from pike and perch, that reach of the River Brathay from which the collections were made is practically free from such enemies. The waters investigated are slightly acid and poor in mineral salts; a study of the growth of the minnow in a richer water might be of interest in relation to the age attained by the fish.

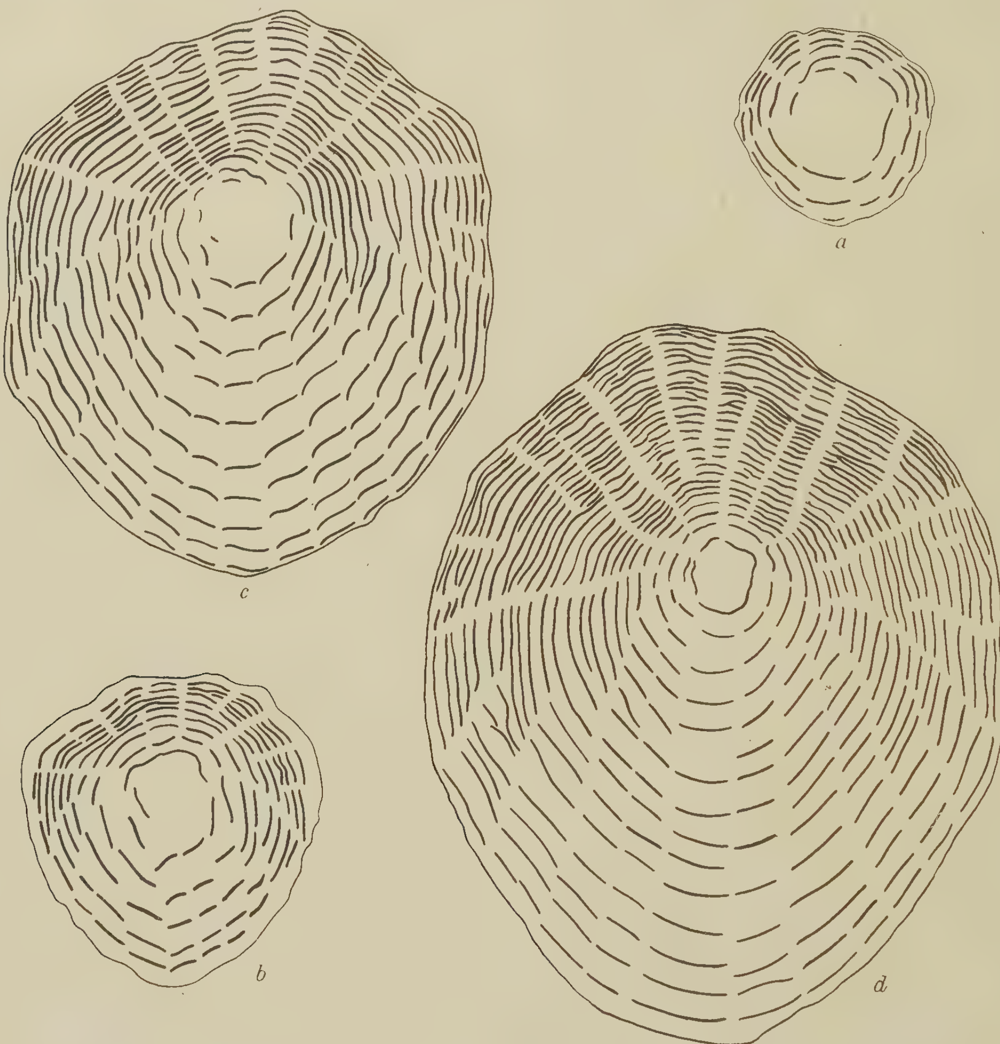

Fig. 3. Scales of minnows. ×85. (*a*) 1 year old (O group). (*b*) 1+ years old, +growth at edge of scale (I group). (*c*) 2 years old (I group). (*d*) 3 years old (II group).

would have been indicated by the presence of more fish. The small number of these larger fish has indeed been apparent throughout the whole investigation. Apparently, therefore, the Windermere and River Brathay minnows die off at an early age or it may be that the older individuals are eaten by other fish (pike, perch, etc.). There seems no reason, however, to think that predators show any preference for older specimens; also although Windermere min-

Weight

In the work on growth, length rather than weight has been used as an index of the size of fish, but in order to ascertain how condition varies in different size groups and seasonally, samples of fish were weighed as well as measured.

The minnows examined for growth rate were almost ready to spawn, and their weights will be

Table 2. *Length (in mm.) for age relationship of Windermere minnows.*
(Number of fish in brackets)

	Age group ...	O	I	II
All fish:	Mean length	33·7 (91)	56·2 (130)	68·8 (65)
	Range in length	24–42	42–68	56–77
	Standard deviation	4·48	5·62	4·32
Males:	Mean length	35·3 (42)*	55·7 (69)	63·9 (15)
	Range in length	26–42	42–66	56–67
Females:	Mean length	33·2 (42)*	56·9 (61)	70·2 (50)
	Range in length	25–41	47–68	58–77

* Sex of seven fish not determined.

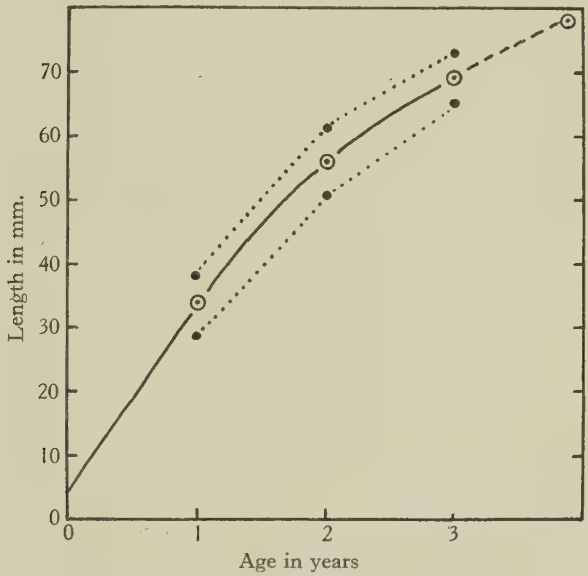

Fig. 4. Mean length of Windermere minnows plotted against age. (Standard deviation indicated by dotted line.)

Table 3. *Length (in mm.) for age relationship of River Brathay minnows.*
(Number of fish in brackets)

	Age group ...	O	I	II
All fish:	Mean length	36·6 (66)	54·4 (106)	65·3 (33)
	Range in length	27–43	41–68	57–74
	Standard deviation	4·51	6·61	4·64
Males:	Mean length	38·3 (30)*	54·0 (53)	62·5 (10)
	Range in length	32–43	41–64	57–66
Females:	Mean length	38·3 (14)*	54·7 (53)	65·6 (23)
	Range in length	30–43	46–68	62–74

* Sex of twenty-two fish not determined.

increased, in the case of the I and II groups, by the ripe condition of the gonad. The value of the following figures, showing the mean weight and range in weight of such Windermere fish, is limited by this consideration: O group, 0·57 g. (0·2–0·9 g.); I group, 2·33 g. (1·0–3·7 g.); II group, 5·27 g. (3·0–6·6 g.).

The larger collections of minnows taken during 1940–1 were weighed in half-centimetre length groups and the average weight for the mid-point of the length group obtained. Data of this kind for April–May and August–September are given in Table 4. In the former period most of the fish of over 38 mm. have full gonads; in the latter reproduction is over and, according to Bullough (1939), there is as yet little increase in the volume of testes or ovaries. The length to weight relationship has also been expressed as a condition factor calculated from the formula $K = 100\,W/L^3$, where L and W are the mean length and weight figures of the table. Among the immature fish the lower condition factor of the August–September specimens is most likely due to the inclusion of fish hatched in the previous May. The growth of such fish would primarily be in length rather than weight. The weight of the mature fish in April–May is, as one would expect from the ripe gonads, appreciably greater than in August–September, and in comparing the value of K at the two periods, the sexual condition must be taken into account. In August–September the condition factor is highest in the 4·3 and 4·8 groups, suggesting that the smaller fish in their second year, probably immature or well-recovered spents, are those in best condition.

Table 4. *Length and weight relationship of Windermere minnows*

		April and May			August and September		
	Mean length in cm.	No. of fish	Mean weight in g.	K	No. of fish	Mean weight in g.	K
Immature	2·3	98	0·17	1·40	—	—	—
	2·8	180	0·27	1·23	8	0·24	1·09
	3·3	109	0·41	1·14	17	0·37	1·03
Mature	3·8	39	0·68	1·24	18	0·70	1·28
	4·3	53	1·16	1·46	61	0·95	1·19
	4·8	67	1·64	1·48	161	1·39	1·25
	5·3	54	2·42	1·62	131	1·73	1·16
	5·8	22	2·81	1·44	34	2·30	1·14
	6·3	15	4·07	1·63	14	2·96	1·18
	6·8	7	4·95	1·58	4	3·50	1·12
	7·3	5	6·02	1·55	—	—	—

(*d*) *Food*

No detailed account of the food of the minnow was available in the literature of this country or the Continent until that given by Tack (1940). In the present investigation 1228 fish from Windermere and 833 from the River Brathay taken in bi-monthly collections over two years* have been examined for food. These specimens, arranged in 10 mm. length groups, are given in Table 5. The variation in the numbers examined both for the different length groups and the months must be borne in mind when results based on the data obtained from the examinations are considered. The methods used for the identification, enumeration and evaluation of the gut contents have been described earlier (p. 140). Details of the food groups into which the gut contents were classified are given below.

Windermere. Surface insects of aquatic origin belonged to the Trichoptera, Ephemeroptera and Plecoptera, their relative incidence in the guts being in this sequence. The caddis flies were not identified, fragments of *Ephemera danica* O. F. Müller were recognized, and of the few Plecoptera eaten *Nemoura* was the only genus determinable. The surface insects of terrestrial origin included Diptera (*Bibio*, etc.), Hemiptera (Aphids, frog-hoppers and tree-hoppers), Hymenoptera (Chalcids, Braconids and ants) and Psocoptera. The Chironomid pupae were usually taken by the minnow during their ascent to the surface. The Copepods eaten were chiefly *Diaptomus*, *Cyclops* and *Canthocamptus*. The Cladocera included *Daphnia hyalina* var. *galeata* Sars, *Bosmina obtusirostris* Sars, *Leptodora kindti* (Focke), *Chydorus sphaericus* (O. F. Müller), *Alonopsis elongata* Sars, *Acroperus harpae* Baird, *Alonella exisa* (Fischer) and *Eurycercus lamellatus* (O. F. Müller). The first three species are planktonic forms, the remainder are usually found amongst weeds. The nymphs of Ephemeroptera identified were *Ephemera danica*, *Leptophlebia*, *Caenis*, and Ecdyonurids. The nymphal Plecoptera recorded were *Nemoura avicularis* Morton and *Chloroperla*. Many of the Tri-

* The two years' lake collections were made from December 1939 to November 1941, those from the river from May 1940 to April 1942. Although the periods do not coincide exactly, the two years are regarded in the tables as 1940 and 1941, in order to avoid unnecessary divisions.

chopterous larvae were not identified, but Leptocerids were frequently noted and *Oxyethira* was recorded and the general impression gained was that the lake minnows contained appreciably fewer species than those of the river. No attempt was made to identify the Chironomid larvae. The 'various Diptera larvae' were chiefly of the Tipulid type, with a few specimens also of *Chaoborus*. The molluscs were fragmentary, but *Ancylus fluviatilis* O. F. Müller was identified and seemed to be the most frequent species; *Pisidium*, *Sphaerium* and *Planorbis* were also noted. The aquatic Oligochaetes were not identified. The category 'Chance Food' was a repository for those plant and animal substances which having by chance reached the water were eaten by the fish; it included earthworms, spiders, centipedes, etc., and in the autumn, quantities of birch seeds; a few minnow eggs found in fish caught in May have also been included in this category. Diatoms were represented by several genera, *Amphora*, *Acnanthes*, *Synedra*, *Tabellaria*, *Cymbella*, *Gomphonema* and *Navicula*, all of which are epiphytic species and usually found in guts which also contained filamentous algae. The category 'plant debris and mineral matter' consisted of fragments of moss and higher plants together with sand and grit which were often found in the guts.

River Brathay. Food eaten in the river was classified into the same groups, though these groups were often represented by different species. Among the surface insects of aquatic origin the Trichoptera were most numerous, but neither they nor the Ephemeroptera were identified; the Plecoptera included *Leuctra hippopus* Kemp and *Protonemura meyeri* (Pictet). The surface insects of terrestrial origin mostly belonged to the Diptera, Hemiptera and Hymenoptera. As in the lake the pupal Chironomidae found in the gut were almost all emerging specimens. The Copepoda included *Cyclops* and *Canthocamptus*, and the Cladocera were almost all *Chydorus*. Nymphal Ephemeroptera were represented by *Ephemerella ignita* (Podon), *Baëtis* spp., *Centroptilum luteolum* (O. F. Müller) and *Ecdyonurus* sp. Nymphs of Plecoptera included *Chloroperla*. A number of genera, *Leptocerus*, *Hydropsyche*, *Agapetus*, *Polycentropus*, *Rhyacophila*, *Lepidostoma*, *Oxyethira*, as well as some Limnophilid forms, were recognized among the larval Trichoptera. The various larval Diptera included *Simulium* and Tipulids. The Mollusca identified were *Ancylus* and *Limnaea*. The chance food frequently included caterpillars. The diatoms represented were similar to those in Windermere and the filamentous algae included *Zygnaema*, *Bulbochaete*, *Mougeotia*, *Oedogonium*, *Hyalotheca* and the red branched form known as *Chantrasia*.

Table 5. *Number of fish in each* 10 *mm. length group examined for food from two years' collections*

Length group	10·5–	20·5–	30·5–	40·5–	50·5–	60·5–	70·5–	Total fish
Windermere								
Jan.	—	20	23	28	11	—	—	82
Feb.	1	36	19	17	8	—	—	81
Mar.	—	25	25	20	5	1	—	76
Apr.	1	29	29	12	27	17	—	115
May	7	20	29	40	27	11	—	134
June	—	21	40	45	21	7	—	134
July	15	8	16	44	46	27	1	157
Aug.	2	26	10	21	31	19	—	109
Sept.	18	50	6	27	40	18	1	160
Oct.	—	28	13	24	25	7	—	97
Nov.	1	4	2	1	—	—	—	8
Dec.	—	27	9	16	18	5	—	75
Total fish	45	294	221	295	259	112	2	1228
River Brathay								
Jan.	—	1	1	3	10	3	—	18
Feb.	—	—	2	5	5	2	—	14
Mar.	—	—	1	8	9	4	—	22
Apr.	—	—	—	25	26	18	—	69
May	—	8	25	58	51	11	1	154
June	—	10	22	42	40	4	—	118
July	—	—	17	49	38	4	1	109
Aug.	29	22	11	35	33	6	—	136
Sept.	—	—	7	20	34	10	—	71
Oct.	—	10	9	24	39	9	—	91
Nov.	—	1	2	3	4	1	—	11
Dec.	—	—	—	7	8	5	—	20
Total fish	29	52	97	279	297	77	2	833

(1) *General food*

In Table 6 and Fig. 5 the percentage composition of the diet based on data from all the minnows

examined is given; Table 6 shows also the points on which the percentages of Fig. 5 are based, and in addition the percentage figure for the two years taken together.

Windermere. It is clear from the two years' data, both separately and collectively, that Cladocera are the chief food; and Fig. 6 shows that the predominance of these organisms is not due to a heavy consumption at any one time, for they form an important part of the diet throughout the year. In

Table 6. *Percentage composition of the diet in* 1940 *and* 1941 *shown for the two years separately and collectively*

Windermere

	Surface insects, aquatic		Surface insects, terrestrial		Chironomidae (pupae)		Hydracarina, Rotifera		Copepoda		Cladocera	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	9	1	112	100	64	31	11	16	257	82	349	291
% proportions	0·6	—	7·3	6·8	4·2	2·1	0·7	1·1	16·8	5·5	22·9	19·7
% proportions for two years	*0·3*		*7·0*		*3·1*		*0·8*		*11·3*		*21·3*	

	Ephemeroptera (nymphs)		Plecoptera (nymphs)		Trichoptera (nymphs)		Chironomidae (larvae)		Diptera (larvae) various		Mollusca	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	96	86	26	5	80	103	77	96	10	3	25	46
% proportions	6·3	5·8	1·7	0·3	5·2	6·9	5·0	6·5	0·6	0·2	1·6	3·1
% proportions for two years	*6·1*		*1·0*		*6·1*		*5·7*		*0·4*		*2·4*	

	Gammarus		Oligochaeta (aquatic)		Chance food		Diatoms		Filamentous algae		Plant debris and mineral matter	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	31	22	5	10	66	71	109	188	121	233	81	96
% proportions	2·1	1·5	0·3	0·7	4·3	4·8	7·2	12·7	7·9	15·8	5·3	6·5
% proportions for two years	*1·8*		*0·5*		*4·6*		*9·9*		*11·8*		*5·9*	

River Brathay

	Surface insects, aquatic		Surface insects, terrestrial		Chironomidae (pupae)		Hydracarina, Rotifera		Copepoda		Cladocera	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	13	6	80	68	47	51	28	16	10	4	13	31
% proportions	1·1	0·6	6·5	6·6	3·8	4·9	2·3	1·5	0·8	0·4	1·1	3·0
% proportions for two years	*0·8*		*6·5*		*4·3*		*1·9*		*0·6*		*1·9*	

	Ephemeroptera (nymphs)		Plecoptera (nymphs)		Trichoptera (nymphs)		Chironomidae (larvae)		Diptera (larvae) various		Mollusca	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	169	100	19	17	105	101	183	174	29	8	6	7
% proportions	13·8	9·7	1·6	1·6	8·5	9·7	14·9	16·8	2·4	0·8	0·5	0·7
% proportions for two years	*11·9*		*1·6*		*9·3*		*15·8*		*1·6*		*0·6*	

	Gammarus		Oligochaeta (aquatic)		Chance food		Diatoms		Filamentous algae		Plant debris and mineral matter	
Year	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941	1940	1941
No. of points	5	12	14	9	39	28	81	112	279	240	105	55
% proportions	0·4	1·1	1·1	0·9	3·3	2·7	6·6	10·6	22·8	23·1	8·5	5·3
% proportions for two years	*0·7*		*1·0*		*2·9*		*8·5*		*23·0*		*7·1*	

terms of total consumption the Copepods rank next in importance, but there is an appreciable difference between the amount consumed in 1940 and in 1941; and in both years feeding on Copepods is practically confined to the early months. The proportion of the food provided by filamentous algae is about the same as that provided by the Copepods, but their consumption is not confined to so few months in the year. Since the diatoms are to a large extent grazed with the filamentous algae they figure in the diet almost to the same extent as the latter. The consumption of aquatic stages of the Trichoptera, Ephemeroptera and Plecoptera is not high; in the case of the last two groups this may be due to the nymphs, collectively and individually is made up of filamentous algae, the proportion being roughly the same as that formed by the Cladocera in the food of the lake minnows; the other vegetable food, diatoms, was of small account. Chironomid larvae make up an appreciable part of the food and are of much more significance than in the lake; the same applies to the nymphs of Ephemeroptera. Larval Chironomids are known to be in great numbers in fluviatile mosses and appear to be readily accessible to fish (Frost, 1939). *Ephemerella ignita* and *Baetis*, the nymphal Ephemeroptera most frequently found in the minnow, are also abundant in river mosses. Larval Trichoptera are fairly well represented both in per-

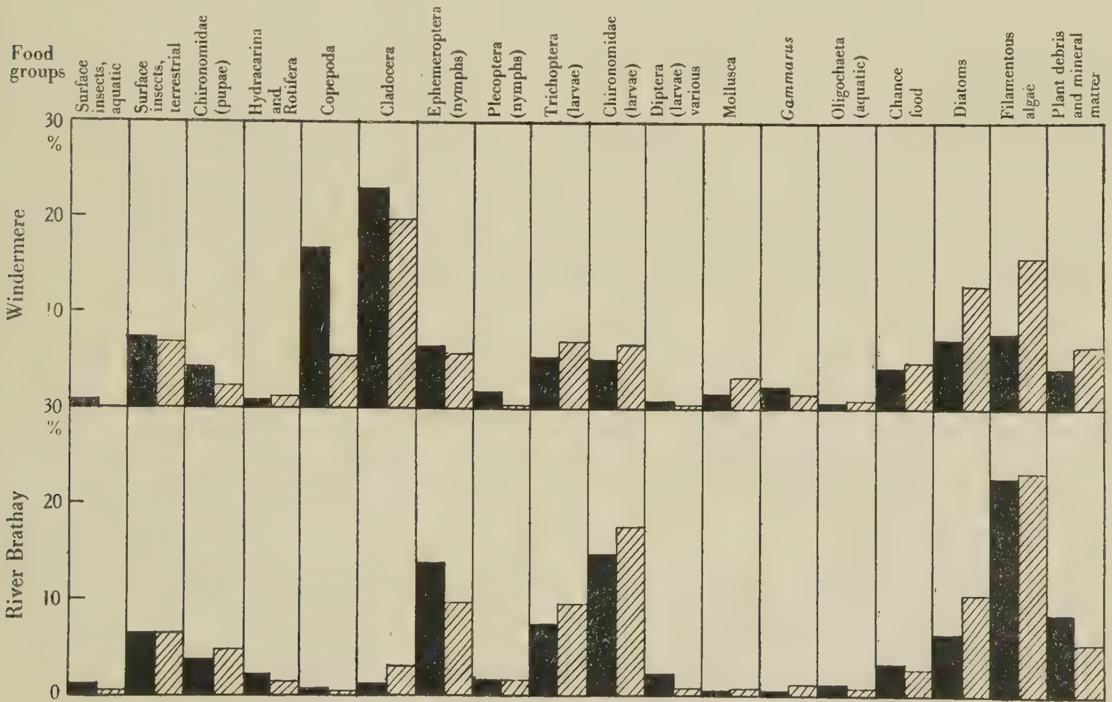

Fig. 5. Percentage composition of the diet of minnows in Windermere and the River Brathay in 1940 (black) and 1941 (cross-hatched).

except those of *Leptophlebia*, being inaccessible except during emergence. Chironomid larvae and pupae are also poorly represented in spite of the abundance of the larvae and the accessibility of the pupae. Surface food is practically all of terrestrial origin. The paucity of *Gammarus* and Mollusca is of interest, since both shrimps and molluscs are common on the lake shore. Minnow eggs occur in the chance food, and although they were found in only a few of the fish examined, it is known from field observation that minnows will feed greedily on their own spawn.

River Brathay. The feeding of the river fish presents some contrasts with that of the lake. The greatest percentage of the diet for the two years both centage proportion and in variety of species. The marked paucity of surface insects of aquatic origin, particularly of the Ephemeroptera, was rather unexpected, since good hatches of these insects occur. The negligible contribution of Cladocera and Copepoda is in sharp contrast to their representation in the lake minnows.

The foregoing account, based on fish captured from typical habitats, may be taken as illustrating in general the feeding habits of the minnow. Local conditions may affect such habits, even in the same body of water, as may be seen from work carried out in Windermere itself. A visiting scientist, Mr Soong, examined the guts of a sample of minnows taken on one day in August 1939 from a quiet backwater

figures in brackets show percentage for two years combined

	Surface insects, aquatic	Surface insects, terrestrial	Chironomidae (pupae)	Hydracarina, Rotifera	Copepoda	Cladocera	Ephemeroptera (nymphs)	Plecoptera (nymphs)	Trichoptera (larvae)	Chironomidae (larvae)	Diptera (larvae) various	Mollusca	*Gammarus*	Oligochaeta (aquatic)	Chance food	Diatoms	Filamentous algae	Plant debris and mineral matter	1940 Fish examined	1940 Fish containing food	1941 Fish examined	1941 Fish containing food
Windermere																						
Jan.	—	—	—	—	3 12 (10)	10 12 (12)	— 10 (8)	14 — (3)	23 9 (12)	— 18 (13)	—	3 1 (2)	14 — (3)	—	— 12 (9)	3 15 (12)	— 10 (8)	30 1 (9)	55	29	27	24
Feb.	—	—	—	—	37 23 (26)	20 2 (5)	13 6 (7)	5 1 (1)	13 2 (4)	5 11 (10)	—	5 2 (3)	—	—	—	2 36 (3)	— 12 (10)	— 5 (4)	24	22	57	56
Mar.	—	—	1 — (1)	—	36 4 (26)	—	3 1 (3)	2 — (1)	2 1 (2)	6 1 (4)	—	1 — (1)	1 1 (1)	—	1 — (1)	27 43 (31)	12 42 (21)	8 7 (8)	60	54	16	16
Apr.	—	1 12 (4)	4 — (3)	3 1 (3)	25 — (19)	6 — (5)	1 1 (1)	6 1 (4)	5 6 (5)	8 11 (8)	—	1 — (1)	6 — (5)	—	1 1 (1)	12 1 (10)	17 38 (22)	4 28 (10)	80	80	35	32
May	1 — (1)	5 1 (3)	2 3 (2)	1 1 (1)	42 6 (25)	39 — (20)	1 4 (2)	— 1 (1)	1 1 (1)	1 — (1)	—	1 3 (1)	1 — (1)	— 1 (1)	— 23 (11)	1 30 (15)	1 8 (4)	3 18 (10)	72	67	62	58
June	3 1 (2)	21 15 (18)	10 9 (10)	— 1 (1)	1 — (1)	38 33 (35)	12 17 (14)	—	3 10 (6)	1 10 (4)	1 — (1)	— 2 (1)	1 1 (1)	—	8 — (5)	—	—	— 1 (1)	84	84	50	50
July	— 3 (2)	19 16 (17)	4 3 (3)	1 4 (3)	— 2 (1)	8 22 (18)	9 6 (7)	1 1 (1)	20 16 (17)	6 6 (6)	1 — (1)	7 6 (6)	—	— 2 (1)	2 3 (3)	6 — (1)	11 10 (10)	7 — (2)	55	48	102	101
Aug.	—	4 2 (3)	7 2 (5)	— 1 (1)	1 9 (5)	53 5 (32)	6 8 (6)	1 1 (2)	5 5 (5)	1 10 (5)	1 3 (1)	2 10 (5)	— 1 (1)	— 3 (2)	6 3 (5)	3 14 (7)	6 14 (9)	4 9 (6)	55	55	54	51
Sept.	—	1 4 (3)	3 — (1)	—	3 — (1)	21 52 (42)	6 — (2)	—	8 1 (4)	13 2 (6)	2 — (1)	8 2 (4)	1 2 (1)	—	3 — (1)	7 1 (2)	16 33 (27)	8 3 (5)	50	45	110	104
Oct.	—	16 10 (14)	6 3 (6)	1 — (1)	3 — (2)	20 42 (26)	7 2 (5)	1 — (1)	1 18 (5)	6 2 (5)	1 — (1)	— 6 (2)	1 2 (1)	3 — (2)	18 2 (13)	1 2 (2)	8 5 (7)	7 6 (7)	59	58	38	35
Nov.	—	10 —	—	—	—	20 —	40 —	—	10 —	10 —	—	—	—	—	—	10 —	—	—	8	6	—	—
Dec.	—	—	1 — (1)	—	29 5 (24)	22 — (18)	12 14 (12)	—	3 14 (5)	10 — (8)	2 — (2)	—	3 38 (10)	—	1 14 (3)	7 — (5)	4 — (4)	7 15 (8)	46	40	29	12
River Brathay																						
Jan.	—	—	—	—	—	—	15 — (10)	—	60 20 (46)	10 40 (20)	— 20 (6)	—	— 10 (4)	— 10 (4)	—	—	—	15 — (10)	10	8	8	3
Feb.	—	—	—	—	—	—	15 5 (10)	5 — (3)	10 37 (23)	15 — (8)	5 — (3)	—	—	—	— 53 (25)	15 — (8)	—	35 5 (20)	15	5	9	9
Mar.	—	2 3 (3)	—	—	11 — (7)	2 — (1)	7 17 (11)	4 — (3)	9 20 (13)	35 17 (27)	4 — (3)	2 7 (4)	2 — (1)	—	—	7 7 (6)	13 26 (18)	2 3 (3)	13	13	9	9
Apr.	—	2 7 (5)	19 3 (10)	—	—	— 1 (1)	20 4 (12)	4 5 (5)	4 10 (7)	22 23 (22)	—	2 — (1)	4 4 (4)	2 — (1)	— 10 (5)	3 13 (8)	3 18 (11)	15 2 (8)	41	32	28	24
May	3 1 (3)	12 15 (12)	3 19 (7)	2 — (2)	2 — (1)	2 2 (2)	9 5 (8)	1 2 (1)	10 2 (8)	23 10 (20)	4 — (1)	1 — (1)	—	1 — (1)	1 4 (2)	2 20 (6)	21 18 (20)	6 2 (5)	95	90	59	44
June	1 1 (1)	7 9 (8)	1 4 (2)	8 1 (4)	— 1 (1)	—	21 10 (15)	1 3 (3)	10 17 (14)	21 20 (20)	2 1 (1)	— 1 (1)	— 1 (1)	2 2 (2)	1 1 (1)	1 15 (8)	22 13 (17)	1 1 (1)	60	60	58	56
July	—	1 6 (3)	5 6 (5)	3 1 (2)	—	4 6 (5)	9 20 (14)	1 1 (1)	2 10 (6)	9 13 (11)	1 2 (2)	—	— 1 (1)	1 — (1)	4 — (2)	14 12 (13)	37 17 (28)	9 5 (6)	63	53	46	45
Aug.	1 1 (1)	7 1 (5)	6 0 (6)	2 5 (4)	—	1 — (1)	31 12 (19)	1 1 (1)	6 1 (3)	13 30 (23)	5 — (2)	1 — (1)	1 1 (1)	3 1 (2)	15 1 (7)	1 8 (6)	6 13 (10)	— 7 (4)	39	38	97	92
Sept.	—	5 7 (6)	5 — (3)	—	—	—	17 7 (12)	3 — (2)	14 6 (10)	8 2 (5)	8 — (4)	1 — (1)	— 1 (1)	—	1 — (1)	8 1 (5)	24 63 (41)	6 13 (9)	27	27	44	30
Oct.	—	8 4 (6)	2 3 (3)	— 1 (1)	—	— 4 (2)	1 3 (2)	1 — (1)	3 2 (6)	— 4 (2)	— 2 (1)	— 2 (1)	—	—	—	21 14 (17)	44 48 (46)	20 4 (12)	38	37	53	44
Nov.	—	7 50 (9)	—	—	—	—	—	— 50 (3)	—	—	—	—	—	—	7 — (6)	7 — (6)	34 — (33)	45 — (43)	10	9	1	1
Dec.	—	—	—	—	—	—	— 5 (3)	—	60 28 (39)	—	—	—	— 5 (3)	—	— 5 (3)	—	— 33 (23)	40 24 (29)	9	5	11	9

which is almost cut off from the lake. This creek is full of aquatic plants and overhung with trees. Mr Soong found filamentous algae to be the main diet, supplemented by winged Diptera, ants and Cladocera.

(2) *Seasonal variation in food*

The seasonal character of the food is shown in Table 7 and Fig. 6. In the table data for 1940 and 1941 are given separately and also for the combined years; in the figure only the first are shown. To obtain monthly data (for each year separately) the points assigned to the different food groups have been expressed as percentages of the total month's points. In Fig. 6 the width of the column represents 100% and the results thus obtained for 1940 (black) and for 1941 (cross-hatched) have been placed in juxtaposition so that the two years should be read separately (not jointly) in terms of 100%. In Table 7 a percentage figure for the month based on data for the two years combined is given. Wide differences in the points gained in 1940 and 1941 may heavily weight this figure. Since, however, the sampling will have been affected by external factors it is unlikely that such weighting has affected the generalized picture.

The figures given at the side of Table 7 indicate that the proportion of fish with empty guts is low throughout the several months of the year in both Windermere and the River Brathay. There is some suggestion of a falling off in feeding in both Windermere and the River Brathay during November, December and January, which is corroborated by the figures given below (Table 8) showing the monthly average number of points gained per fish during the two years.

Table 8. *Average number of food points gained per fish in each month*

Month ...	Jan.	Feb.	Mar.	April	May	June
Windermere	1·47	2·9	3·61	2·93	2·7	2·79
River Brathay	1·67	2·78	3·45	2·16	2·29	3·33
Month ...	**July**	**Aug.**	**Sept.**	**Oct.**	**Nov.**	**Dec.**
Windermere	2·41	2·34	2·38	2·24	1·25	1·5
River Brathay	2·83	2·92	2·67	2·97	3·0	1·55

The low figures for the winter months may represent a slowing up of the digestive processes as well as a reduction in the amount eaten. It is evident, however, that the inactivity of the minnow, which coincides with these months, is not accompanied by fasting.

Windermere. In the lake the seasonal changes in the food are what might be expected from the known habits of the minnow, active and pelagic in summer, passive and benthic in winter. Thus among the Cladocera, which constitute a large proportion of the food throughout the year, two planktonic forms, *Bosmina obtusirostris* and *Daphnia hyalina*, are prominent in the stomachs from May to October but are replaced from November to April by *Eurycercus* and *Acroperus*, two forms of more or less benthic habit. The Copepods, which are important in the diet from December to May, show a similar relationship to the habit of the minnow; in May the fish are gorged with *Diaptomus*, in the other months *Canthocamptus* and *Cyclops* chiefly are consumed. There is a consistent and appreciable consumption of filamentous algae and diatoms from January to April, a period when the algal flora would provide an easily available food on the lake bottom. The subaquatic forms of Trichoptera, Ephemeroptera, Plecoptera and Chironomidae are eaten throughout the year and show no significant seasonal variations in the amount consumed. Terrestrial insects are recorded from the fish at times when such surface food would be most available. The relatively high consumption of *Gammarus* during winter may be correlated with the minnow's retirement under stones at this time.

River Brathay. In drawing conclusions about seasonal changes in the food it must be remembered that from December to February the data are few and therefore relatively insignificant. Filamentous algae, the chief food, occur in appreciable quantity through most of the year and, since it seems unlikely that any change in the seasonal abundance of these algae would be sufficiently great to affect the minnow's supply, it may be assumed that the fluctuations indicated are fortuitous. Aquatic stages of Ephemeroptera, Chironomidae and Trichoptera (particularly the first two) make a steady contribution to the diet throughout the spring, summer and autumn, and from the data available the last group would appear to form a large part of the winter diet. Fluctuations in the numbers of Ephemeroptera may be related to the habits of the species eaten, as is shown by *Ephemerella ignita*. In June, July and August, when this species predominates in the diet, the nymphs are well grown and active or emerging, and are thus more accessible to fish than at any other time. Plant debris and mineral matter are always available and no significance attends their seasonal fluctuations in the guts. The remaining food groups show no marked seasonal variations.

(3) *Food of different length groups*

All the minnows examined for food have been divided into four 20 mm. length groups, 0–20·5, 20·5–40·5, 40·5–60·5 and 60·5–80·5, which correspond, roughly, to the 'larval' or 'pin' stage and O-, I- and II-year groups respectively. The food taken by each such group is shown in Fig. 7, in which the points given to each food group have been totalled for each length group and such points expressed as a percentage. The variation in the number of fish examined for any month or any length group must influence the result. Such is particularly marked in the 0–20·5 and 60·5–80·5 groups; it is likely, however, that some of the differences apparent from Fig. 7 are significant.

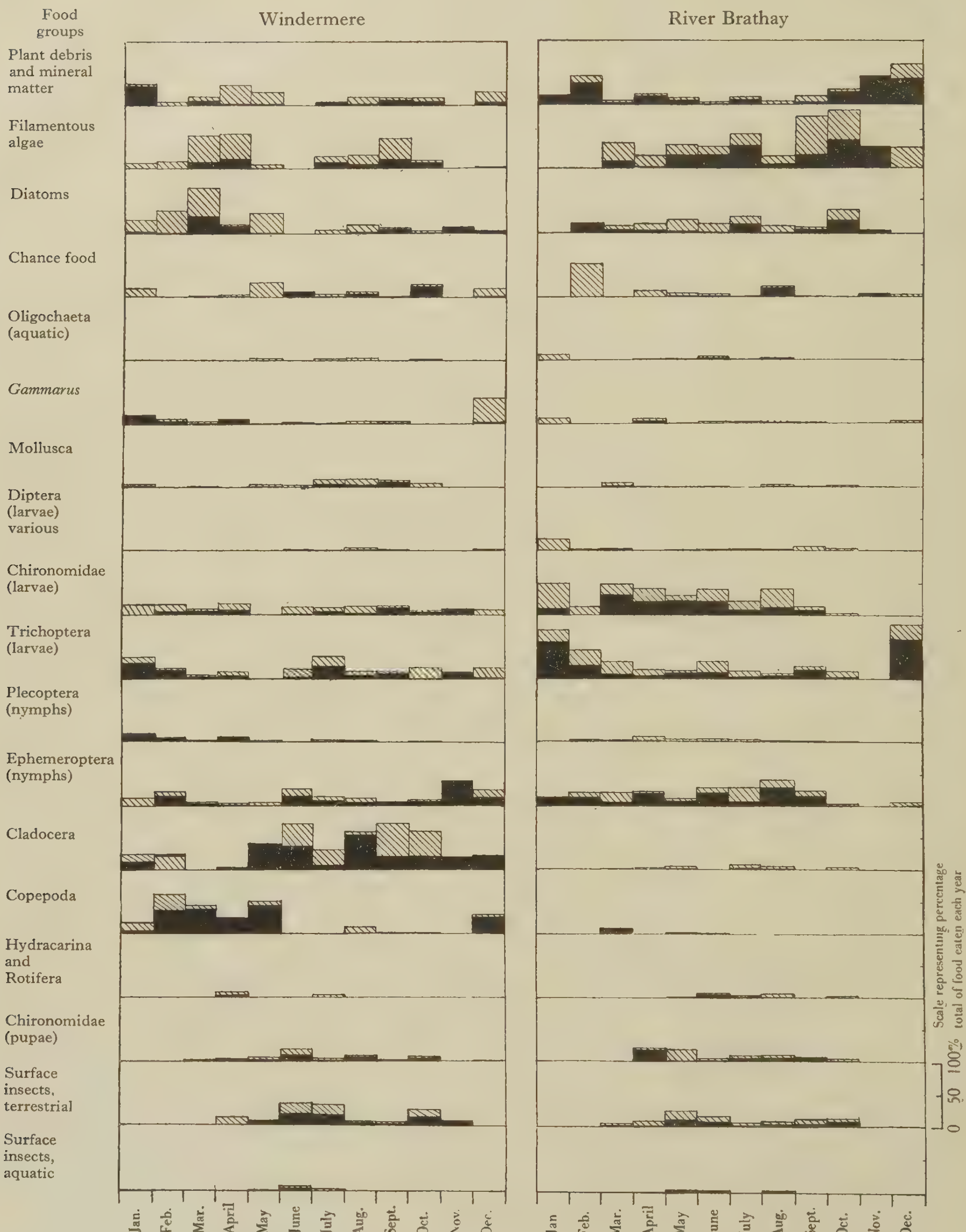

Fig. 6. Percentage composition of diet in different months in 1940 (black) and 1941 (cross-hatched).

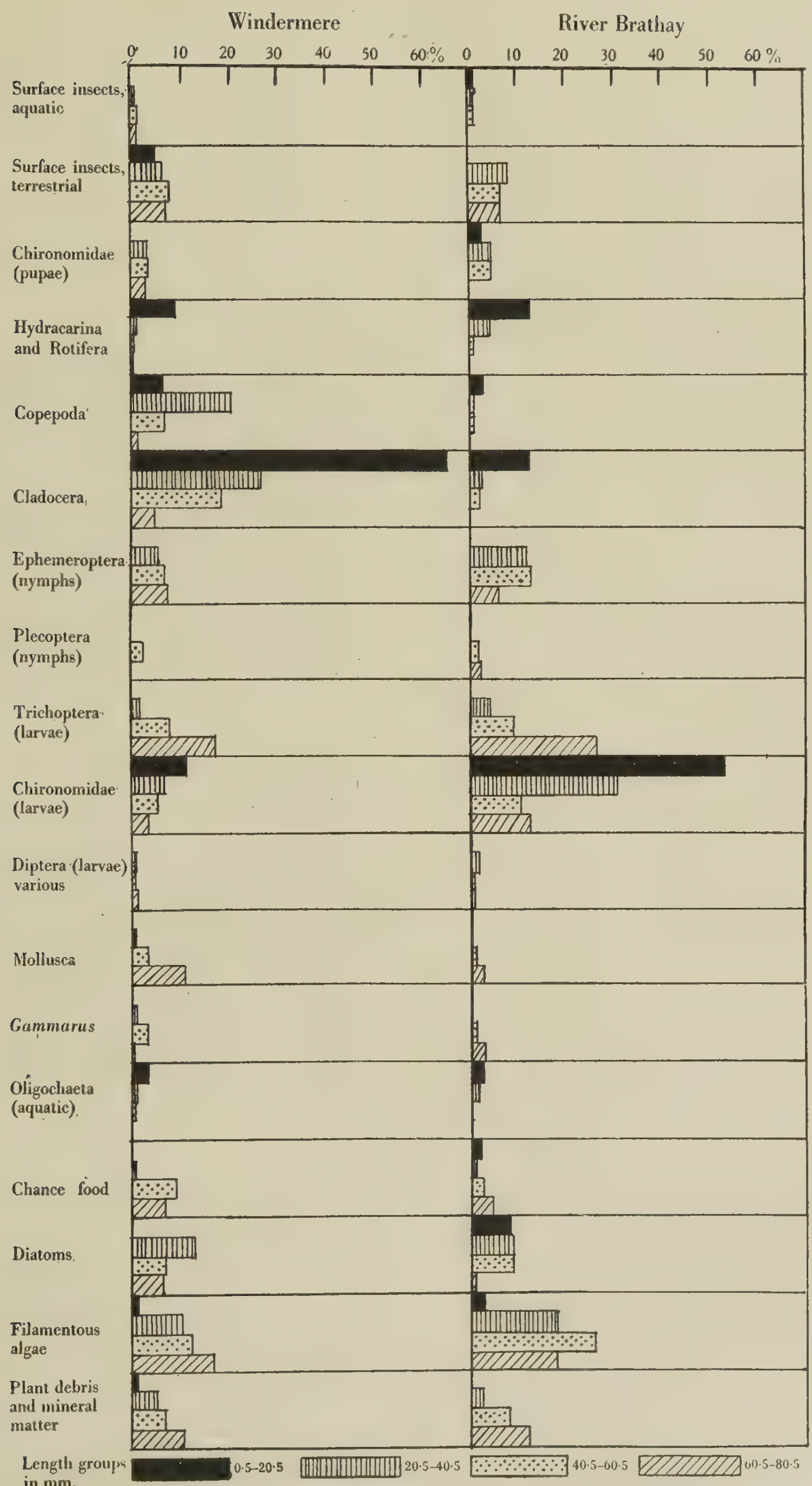

Fig. 7. Percentage composition of diet of four different length groups.

In both Windermere and the River Brathay most of the food organisms may be eaten by fish of any length group, but their proportional representation differs with the length group.

Windermere. The smallest length group appears to feed mainly on small animal food, Cladocera, Copepoda, rotifers and mites. This result may, however, have been affected by the fact that the fish were captured in February, May, July, August and September only. The two succeeding groups show a more varied diet in which, although Cladocera predominate, other animal and plant foods play an important part. In the fourth group Cladocera are of little consequence, the minnows feeding on larger animals such as larval Trichoptera, nymphal Ephemeroptera, and Mollusca and on filamentous algae.

River Brathay. In the smallest length group, represented by one collection only, taken in July, Chironomid larvae predominated and Cladocera, mites and rotifers were present to some extent. Chironomid larvae, found in appreciable numbers in all the fish, are the chief food of the second length group. Except in the smallest length group, the food consists of a variety of animals and plants with a tendency to an increase in the consumption of nymphal Ephemeroptera and larval Trichoptera with the increasing length of the fish. Filamentous algae and diatoms are eaten to an appreciable extent by all the minnows over one year old.

These observations are in some agreement with those of Stankovitch (1921) who found that, in Alpine streams, minnows of 8–18 mm. fed mainly on rotifers, which are replaced in the older ones by aquatic insect larvae, particularly Chironomids.

Thus, in Windermere and the River Brathay, the only significant difference in the diet of minnows of different lengths is the tendency for an increase in the consumption of larger animal foods as the fish increase in length. Such food is probably more easily captured by the bigger minnows and may provide a meal which is more satisfactory and obtained with less effort than one of smaller organisms.

The food of the minnow may be divided into surface, mid-water and bottom feeding. Based on the order in the tables the first two food groups may be regarded as the first type, the next four as the second, and the remainder as the last. Fig. 8 shows the points assigned to each month, divided into these categories and expressed as percentages of the total points (the two years are considered together). In Windermere, bottom food predominates in the winter and early months of the year; the increase in mid-water feeding from April to October coincides with the great increase in the planktonic Crustacea which marks this time, and surface food is insignificant except in midsummer. In the River Brathay, bottom feeding forms more than 70% of the food each month, but there is an increase in surface and mid-water food in late spring and early summer due to the greater number of large insects and emerging aquatic forms.

The results obtained from the gut contents of the Windermere and River Brathay minnows may be compared with those given by Tack (1940) for the 344 fish of the Albaumer and Lenne streams. He found that Entomostraca, chiefly Cladocera, predominated in the diet with Chironomid larvae (and some pupae) next in importance; aquatic insect larvae, *Limnaea* and filamentous algae were fairly well represented. In the River Brathay, a flowing water and thus more comparable with Tack's streams, Cladocera were negligible and filamentous algae preponderant; Mollusca were practically absent. The importance of the Entomostraca has a parallel in the Windermere fish, where, however, there is a slight falling off in their consumption in the I-year group and an appreciable one in the oldest class; in Tack's fish Entomostraca predominate in all age groups.

Fig. 8. Percentage proportions of surface, mid-water and bottom food in diet throughout the year.

Internal parasites. It was noted during the gut examination that very few of the minnows were in-

fected with internal parasites. A small trematode* *Bunodera* sp. and more rarely a nematode were found in the alimentary canals of some fish. Tack remarks on the paucity of parasites, that most frequently occurring being *Neorhynchus rutili*, an Acanthocephalan not noted in the Windermere or River Brathay minnows.

Food of trout fry. The results obtained from the examination of the gut contents of fifty trout (*Salmo trutta*) fry from the River Brathay taken in April (2), May (23), June (12), July (2), August (3), September (3) and December (5) (p. 142) are given below in Table 9; figures for the minnow from Table 4 are given for comparison. The chief foods of the trout are the nymphs of Ephemeroptera and Chironomid larvae; both of which form a high proportion of the diet of the Brathay minnows.

Table 9. *Percentage composition of diet of fifty trout* (Salmo trutta) *fry from the River Brathay.* (*Data for the minnow are given in brackets*)

Food group	Surface insects, aquatic	Surface insects, terrestrial	Chironomidae (pupae)	Cladocera	Ephemeroptera (nymphs)
% composition	5·6 (0·8)	8·1 (6·5)	7·1 (4·3)	1·0 (1·9)	25·4 (11·9)

Food group	Plecoptera (nymphs)	Trichoptera (larvae)	Chironomidae (larvae)	Diptera (larvae) various	*Gammarus*
% composition	9·7 (1·6)	12·2 (9·3)	27·9 (15·8)	1·0 (1·6)	2·0 (0·7)

(*e*) *Reproduction*

The sex, determined by internal examination, was noted for all those fish examined for age determinations and for the majority examined for food. The latter, which had been chosen mostly without regard to sex, showed that, in Windermere, of those more than 40 mm. long, that is, fish which were most likely sexually mature, 63% were females and 37% were males; a similar sex ratio also held for minnows of less than 40 mm. long, most of which would be immature specimens. Among those fish used for age determinations the paucity of males was particularly noticeable in the 3 year olds, for in a collection of about 100 fish of this age the males were outnumbered by the females by 7 to 1.

The preponderance of females in a minnow population may be explained by presuming that they tend to live longer than the males, but it may also be that sex reversal, as shown by the work of Bullough (1940), is to some extent a contributory factor. In a sample of 414 minnows from Windermere, Bullough identified 183 as males, but in 10% of these, 57–64 mm. long and probably in their third year, he found, from microscopic examination, that the gonads contained both testicular and ovarian tissues in varying amounts, suggesting stages of transformation from a female to a male type. He concluded that 'a change of sex was taking place in these fish. Minnows which had apparently been functional females, were in their old age becoming transformed into functional males.' He found that smaller minnows from Windermere were not hermaphrodite, but induced evidences of sex reversal in them by the injection of testosterone propionate into the female and oestrin into the male. In his discussion he says: 'The process of sex reversal in these older female minnows closely resembles that described by Witschi (1932) in older female frogs of "undifferentiated races". The males resulting from this sex change would be, like the frog recorded by Crew (1921), genetically females, and consequently all their offspring would be females too. Although all the older female minnows do not appear to undergo sex reversal, the last consideration may help to explain the usual preponderance of female minnows over males.' Since the proportion of female minnows which undergo sex reversal would seem to be very small this factor would not appear to be greatly significant in accounting for the predominance of females in Windermere.

The condition of the gonad, as well as the sex, of the Windermere and River Brathay minnows was noted. Those which would not spawn during the coming season were called 'immature', those likely to reproduce during the ensuing season were called 'ripening', or if practically on the point of doing so 'ripe' and those which had already spawned were 'spent' fish. Far more fish were examined for food than for age, and thus there are more data giving the length to sexual condition relationship than there are for that of age to sexual condition. The two sets of data, however, considered together, give a fairly complete picture of the reproductive cycle of the minnow.

Among the fish of the O group, which range in length from 24 to 42 mm., those of 35 mm. and less were almost all sexually immature, as were some specimens above this length, but others, males and females, were ripening to spawn during the coming season. This difference in condition no doubt reflects the protracted breeding time, May to July, the first type being products of the later spawners, the second of those fish which spawned early in the season. The majority of the minnows of over 42 mm., that is, of more than one year old, were sexually mature, although there were some individuals, males and

* Identified by Miss N. Sproston, Cambridge.

females, of about 41–45 mm. long and in their second year of life which were immature. Tack's conclusions about the breeding age of the minnow are much like my own.

The egg of the minnow when just ready for extrusion measures about 1·3–1·4 mm. in diameter. The number present varies with the size of the fish. In two-year-old specimens of 42–50 mm. long there were from 105 to 200 eggs per fish, minnows of the same age but of 51–60 mm. contained from 180 to 330 eggs, and three-year-old fish of 61–70 mm. had from 293 to 550 ova to the fish. These counts refer only to the ripe eggs of the ovary. Bullough (1939), who gives a detailed histological account of the seasonal changes taking place in the gonads, says 'immediately after spawning both testes and ovaries are slight almost threadlike organs. Very little growth takes place through the summer months, but during late September and early October there is a considerable increase to about nine times the original volume in the case of the ovary and to about three times in the case of the testes. The volume thus attained remains fairly consistent throughout the winter and a final increase takes place in the following spring'.

The factors influencing the development and maturation of the gonads of the minnow have been studied under experimental conditions by Bullough (1939, 1941). In the first of these experiments he showed that, in both sexes in winter, a high temperature of 17° C. allows the early maturation stages started the previous summer to continue, but that long periods of artificial light, in addition to the high temperature, were necessary to induce the formation of ova and spermatozoa. In his later experiments he found that, in the spring, the restriction or absence of light delayed the development of the ovaries and slightly retarded that of the testes, but by June it was clear that in both sexes such limitations had failed to prevent sexual development. Bullough therefore postulates that 'an internal reproductive rhythm exists within the minnow and that this internal rhythm is capable of acting in the absence of those external seasonal changes which may normally reinforce it and render it more precise in its time of action'.

Field observations for Windermere and elsewhere indicate that the greatest reproductive activity occurs during the first fortnight in May. Many of the lake fish ripen in June, and the latest date on which eggs collected from a small stream running into Windermere was 25 July. The spawning period of the minnows in the Albaumer Bach as noted by Tack is the same as for Windermere fish; whereas in the Carpathian streams investigated by Vladykov (1927) reproduction went on from the end of March to 15 October. The condition of spent fish in Windermere, particularly of females captured in late May, indicates that all the eggs are shed at one time, and thus the long-drawn-out breeding time is not due to the same individuals shedding their eggs and sperm during a protracted period but to a population composed of fish which mature at different times from May to July, the time of maturity probably being conditioned by that of the hatching from the egg.

Minnows migrate from lakes into running water to lay their eggs, such migrants having been observed in large shoals in the River Brathay and other streams.* River minnows also move to suitable spawning sites, sometimes up side streams. The males may precede the females. The presence of minnow spawn under stones on the shore of Windermere just off a stream mouth, and the capture of 13 mm. minnows ('pins') in the lake far from any inflow from which they might have migrated suggests, however, that all lake fish do not necessarily enter running water to breed.

Spawning habits were observed on 3 May (1942) at about 4.30 p.m. G.M.T., in the River Brathay at a place some three-quarters of a mile from its outflow into Windermere. The river was low and the temperature of the water 58° F. The minnows, which were in great numbers, were in the gravelly, fairly swiftly flowing shallows at the side of the stream. The whole mass of them, consisting of many males and a few females in their bright spawning livery, was in a constant state of activity, swimming, twisting and turning in the current; occasionally some of the fish left it for the quieter water at the side of the stream, where they disappeared under fist-sized stones. Presumably oviposition occurred then, since egg-masses, of 10–20 ova, were found attached to the underside of the stones and male and female fish darted from beneath on being disturbed. Oviposition would also seem to take place in the swift water, as evidenced by the many eggs found among the gravel there. On 5 May spawning shoals were still at the same place, but by the end of the week the number of fish had greatly diminished. There was a marked preponderance of males on the spawning shallows, as was also observed by Mottram (1922). In reference to this he records that the males remain there all the time, whereas the females collect in a pool below and only visit the spawning beds a few at a time, returning afterwards to the pool.

Newly deposited minnow eggs are dirty white in

* Mr C. Myers drew my attention to the pertinacity of the minnows in their attempt to reach their spawning ground, by taking me to witness a most striking example of this in a stream leading into a small lake in West Lancashire. On 15 May (1942) the ripe minnows were seen leaving the lake in hundreds and travelling up the stream across which, at the upper end, a tiny wooden dam 6–7 in. high had been fixed, thus forming a pool above in which the minnows spawned; in the dam a gap of some 6 in. wide and 2 in. deep had been cut, forming a fish 'pass' to the pool. The fish, males and females, on reaching the dam, without any hesitation began to ascend the pass, some leapt into the air and fell on to the pool on the far side, many made several attempts to negotiate the dam by various methods before finally reaching the pool; at the end of one hour all had entered it.

colour and 1·5–1·8 mm. in diameter. Ova taken from the River Brathay were brought into the laboratory on 5 May and some of them hatched on 7 and 8 May. Since the eggs were taken from places where minnows had been observed to spawn on 3 May it is likely therefore that the ova took 4–5 days to hatch. Mottram found that the ova of artificially spawned minnows took 4 days to hatch. Eggs found on 25 July, in a beck flowing into Windermere, were brought into the laboratory where they hatched and the fry were reared. The newly emerged fry, which ranged from 4·2 to 5·0 mm. in length from head to tail, were colourless except for a large, round, pale yellow yolk sac; from birth they were most active. When 2 days old and 6·5 mm. long the yolk sac had elongated somewhat and the eyes were greyish black. On the fifth day some black pigment appeared on their sides, and when 11 days old a green-gold as well as black colouring appeared on the back and sides. The yolk sac had disappeared by the time the 'pin' minnows were 13–14 days old; they were then 8·0 mm. long. Tack (1940) also notes that the 'larvae' lost their yolk sacs at this size. The captive fish grew slowly and when 12 weeks old were only 12 mm. long, well-pigmented dorsally and laterally, with a more or less colourless latero-ventral surface. Some of them lived until 7 November when, at the age of 15 weeks, they measured 12–13 mm. The length attained by this time seems very little, and it may have been due to their being reared in captivity, but that this is probably their normal growth rate is evidenced by the capture of minnows of only 23–24 mm. long on 29 December, specimens which, from a knowledge of the spawning times, could not have been hatched any later than the July in which the ova of the reared fish were collected. The young fish swim in shoals in quiet backwaters; one such, observed in late August, was composed of individuals of from 9·5 to 16 mm. long. Stages in the development of the minnow are shown in Fig. 9; the drawings of (*a*) and (*b*) are from living specimens, those of the remainder from preserved material.

Fig. 9. Development of the minnow. (*a*) Newly hatched, 4·5 mm. (*b*) 2 days old, 6·2 mm. (*c*) 10 days old, 7·0 mm. (*d*) About 6 weeks old, 9·5 mm. (*e*) About 10 weeks old, 11·5 mm. (*f*) 16·0 mm., probably 5 to 6 months old. (Yolk sac, present in (*a*), (*b*) and (*c*), indicated by dense stippling.)

4. DISCUSSION

Some of the ecological factors which affect the minnow will have been apparent in the foregoing account of its natural history, but discussion of most of these factors would be sterile until similar information is available for other localities. In the case of feeding habits, however, sufficient data are available to give some definition of the ecological position of the minnow in relation to other fish. The relationship may best be illustrated by reference to Windermere and the River Brathay where something is known of the fish associations.

Allen (1938) shows that the food of brown trout (*Salmo trutta*) in Windermere consists, according to the season, of *Limnaea*, *Gammarus*, *Asellus*, Chironomid pupae, *Nemoura* nymphs, larval *Leptocerus* and terrestrial insects, none of which organisms are eaten to any extent by the lake minnows. Investigation of the food of brown trout fry in the River Brathay (p. 157) has shown that their chief foods are nymphal Ephemeroptera and Chironomid larvae, organisms which form a high proportion of the diet of the minnows of that river. The greater part of the diet of perch (*Perca fluviatilis*) of less than 16·5 cm. long in Windermere consists of planktonic Crustacea, including *Bosmina*, *Daphnia*, *Diaptomus* and *Cyclops* (Allen, 1935); and other investigations now in progress show that the first two forms predominate in the food of the char. Such organisms, particularly the Cladocera, are the principal food of the lake minnow. The pike (*Esox lucius*), examined by Allen (1939), were all of 30 cm. and over in length, and their diet contained but few creatures that are eaten by the minnow. Work now being carried out on the food of adult eels in Windermere shows that the greater part of their diet consists of aquatic insect larvae, *Gammarus* and Mollusca, which foods are of little importance to the lake minnow.

Thus the evidence from Windermere shows that the planktonic Crustacea, which form the chief food of the minnow, also occur to a considerable extent in the diet of other fish in the lake. Since, however, the supply of these organisms is enormous and the minnow's inroads upon them will be limited by its inshore habits, it seems unlikely that the minnow is a serious competitor for food in this fish community. In the River Brathay much of the minnow's diet is similar to that of the young trout and although, without some estimate of the available food supply, it cannot be accepted that competition between the species will result, it may be assumed that such is more than likely, since an appreciable population of minnows share the same habitat with the trout.

Comparison of the food requirements of the Windermere and Brathay minnows with those of fish from other waters, although of necessity indirect, throws further light on this aspect of the minnow's ecology. The trout of Lough Derg (Ireland) feed heavily at times on planktonic Crustacea (Southern, 1935) which are also an important food of the fry of tench (*Tinca tinca* (L.)), bream (*Abramis brama* (L.)), pike and perch of that lake (Southern & Gardiner, 1926). Investigations carried out by various workers on the food of young salmon show that they feed extensively on aquatic insect larvae. On the River Leven (Windermere) elvers were found to have been feeding solely on Chironomid larvae. Hartley's account (1940) of the food of 'coarse fish' of Cambridgeshire and other waters shows that much of the food of the bream, silver bream (*Blicca bjoernka* (L.)), roach (*Rutilus rutilus* (L.)), ruffe (*Acerina cernua* (L.)) and dace (*Leuciscus leuciscus* (L.)) consists of planktonic crustaceans, aquatic insect larvae and filamentous algae. The evidence from these different waters supplements that from Windermere and the River Brathay, in that it indicates considerable overlap in the food requirements of the minnow and the other fish sharing the same body of water.

The minnow's position in a fish community will be affected by its own value as a food organism. In Windermere Allen found that it was eaten by 'a few trout of all sizes', that the fish diet of perch of over 16·5 cm. long contained a high proportion of minnows, but that the pike, which is largely piscivorous, ate very few. A fair number of eels from Windermere and Esthwaite Water were found to contain minnows. Evidence from other British waters, the Tees and River Itchen (Pentelow, 1932), Lough Derg and River Shannon (Southern, 1935), River Don (Neill, 1938) and River Liffey (Frost, 1939) indicates that the minnow forms only a small part of the food of the brown trout, and Hartley (1940) found fish to be absent from the diet of all 'coarse fish' except pike, perch and eels. Among Continental workers Dyk (1934) found that 16% of the trout of Bohemian streams contained fish, chiefly minnow. André (1935, etc.) notes a paucity of fish in the trout of Canton de Berne rivers, and Stankovitch (1922) remarks that very few of the trout of alpine streams feed on minnow but that it is well known that lake trout do so. Such evidence, to which could be added that to be found in the writings of many other workers, indicates that the value of the minnow as a fish food is not yet decided.

It is clear from the foregoing evidence that the ecological position of the minnow, as conditioned by the food factor, varies greatly with the type of fish association of which it is a member. In large lakes, like Windermere, with a mixed fish population, its feeding habits and limited distribution make it unlikely that it ranks as a serious competitor for food, and it is of itself an appreciable source of food for larger fish. In running waters inhabited primarily by salmon and trout the food requirements of the minnow coincide closely with those of the salmonids and the possibility of serious competition is great. In waters populated predominantly by 'coarse fish' other than pike, perch and eels, the minnow is a non-

contributory, and may become a competitive, element in the food chain.

The conclusions reached in the preceding paragraphs have a practical value in that they suggest a policy towards the minnow in fishery conservation. In general, provided the fish population is balanced with active predators to keep their numbers in check, it may be said that minnows are not inimical to a fishery. But it often happens that in managing a fishery, the balance is disturbed with the object of encouraging a certain species, such as the trout or salmon, and the exclusion of the more active predators like pike and perch. In such conditions the capacity for minnows to multiply is so great that they are dangerous. Therefore in large lakes, such as Windermere, containing salmonids, eels, pike and perch, minnows in reasonable numbers would not be detrimental, and might even be beneficial as providing a food supply. In a small body of water, however, holding a similar community, the minnow's consumption of food might outweigh its value as a food organism. In a salmon or trout river or stream, minnows in any numbers are almost certainly undesirable, as are they also in small lakes and tarns kept primarily for trout fishing. In bodies of water conserved primarily for dace, roach, bream, and so on, the minnow is no asset and may be harmful.

Mention may be made of some economic uses of minnows. In south Germany they are much used by fish farmers as a food for stock trout, a practice which might prove worth while in this country. It is well known that preserved or in the natural state they are an effective bait for angling. It is possible also to use them as bait for long-lines in lakes. Minnows are not now accounted as food for man in this country although formerly they were so regarded, and as late as the mid-nineteenth century they were eaten in quantity in Germany.

5. SUMMARY

1. The natural history of the minnow (*Phoxinus phoxinus* (L.)) has been studied from fish collected and observed in Windermere and one of its affluent streams, the River Brathay.

2. Bi-monthly collections for two years from Windermere yielded some 2600 specimens and from the River Brathay over 1800 for examination.

3. The external features of the minnow are described and sexually dimorphic and breeding characters are noted.

4. Minnows are active and pelagic from April to October and migrate into deeper water where they are relatively passive and hidden under stones from November to March.

5. Length-frequency curves supported by scale examinations indicate that there are certainly three year classes and suggest the possibility of a fourth. In Windermere the growth rate determined from the scales shows the mean length achieved to be 33·7 mm. at the end of the first year (O group), 56·2 at the end of the second (I group), and 68·8 at the end of the third year (II group). The males of the II group are considerably smaller than the females. The growth rate of the River Brathay fish does not differ significantly from that of Windermere. Comment is made on the short-lived character of these fish.

6. In Windermere Cladocera are the main food, with Copepoda, filamentous algae and diatoms forming an appreciable part of the diet. In the River Brathay the fish feed chiefly on filamentous algae, with Chironomid larvae next in importance and larval Trichoptera and Ephemeroptera eaten in significant quantity.

7. Seasonal differences in the quality and quantity of the food taken have been noted and it has been found that there is some variation in the diet of fish of different lengths.

8. The breeding season extends from May to July. Sexual maturity is reached by a few minnows at the end of their first year; the majority of those in their second year and all older fish are mature. The development of the young fish is described.

9. The influence of the minnow's food habits on other associated fish is discussed, and its ecological relations with them defined.

10. Certain practical measures in fishery management, based on this definition, are suggested.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1941–42*

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(With 4 Figures in the Text)

1. GENERAL RESULTS

During 1941–42 arctic fox (*Alopex lagopus*) continued to increase generally throughout the Arctic and Subarctic except for the western coast of Hudson Bay where they had apparently passed their peak.

Lemmings (*Lemmus, Dicrostonyx*), on the other hand, appeared to have 'crashed' throughout much of the Eastern Arctic with the main exception of south and central Baffin Island. On Victoria and King William Islands in the Western Arctic they were still increasing.

Along with the decrease in lemming population snowy owls (*Nyctea nyctea*) had disappeared from northern Baffin Island and northern Quebec and had appeared along the coast of Labrador and at the southern part of James Bay.

2. POPULATION CHANGES

(*a*) *Lemmings*

In northern Quebec and the far north of Baffin Island (groups 2 and 7) lemmings mostly crashed in 1941–42 following two years of increasing abundance. Thus 1940–41 was a peak year for lemmings in these areas—three years after the preceding peak in 1937–38. In southern Baffin Island (group 6) lemmings were still abundant, whereas in 1938–39 they crashed along with those of the northern part of the island.

Pond Inlet. 'In the early spring of 1941 lemmings were very plentiful, but during the winter of 1941–42 became very scarce, and at this date (May 31, 1942), there is practically none around at all.' (A. T. Swaffield.)

Cape Dorset. 'Lemmings still around and so are foxes. Expect them to breed in vicinity.' (O. M. Demment.)

In the preceding cycle the coast of Northern Labrador (group 1) lagged behind northern Quebec and had its peak one year later. In 1941–42 there were only two (conflicting) reports on lemming abundance in this region, but as 'mice' were increasing or abundant at four places it seems likely that there had been a second year of recovery in small rodents.

'Mice' were also said to be increasing or abundant in six reports out of ten for the southern part of Hudson Bay and James Bay (group 3). This was a continued improvement of conditions.

Lemmings had also crashed on the west coast of Hudson Bay (no reports of increase in group 4). There seems to have been a four-year lemming cycle in this area—two years of low density followed by two years of recovery, the last crash year being 1937–38.

Eskimo Point. 'Lemming and mice non-existent in May 1942 and very scarce in fall of 1941.' (W. C. Brownie.)

Lemmings were still reported as abundant on Southampton Island where they had been increasing ever since 1937–38, so that 1941–42 was the fifth year of increase. However, at Repulse Bay (where increase had also been continuous since 1937–38), the report of *decrease, neither abundant nor scarce*, indicates that here the downward swing had set in.

(*b*) *Arctic fox*

The Arctic fox map for 1941–42 gives a very clear picture of increasing abundance everywhere throughout the Arctic and Subarctic except for the west coast of Hudson Bay and the Mackenzie River delta, but upon analysis of the reports with reference to those of previous years it is seen that this increase is of one, two or three years' standing.

1. The expected improvement in white foxes along the Northern Labrador coast had materialized with all but one observer reporting increase. It will be interesting to see if this increase was maintained during 1942–43 when it is likely that foxes crashed in northern Quebec and Baffin Island.

Davis Inlet. 'Both white and coloured foxes were exceptionally plentiful in this vicinity latter part of April and May, and to date (May 28) seem to be remaining, presumably to breed.' (W. R. Bull.)

With so much increase to the north it is not surprising that foxes should also have increased along the south part of Hudson Bay and around James Bay. In this region, which is largely outside the breeding range, recovery had been very abrupt and was probably due to migration from farther north as well as to the fair abundance of 'mice'. The last good year (1937–38) was followed by three poor ones when in each year only one out of eight reports noted increase, whereas in 1941–42 the proportion had risen to six out of eight.

Great Whale River. 'White and coloured foxes quite plentiful during this past winter. Indians inland killing

* Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

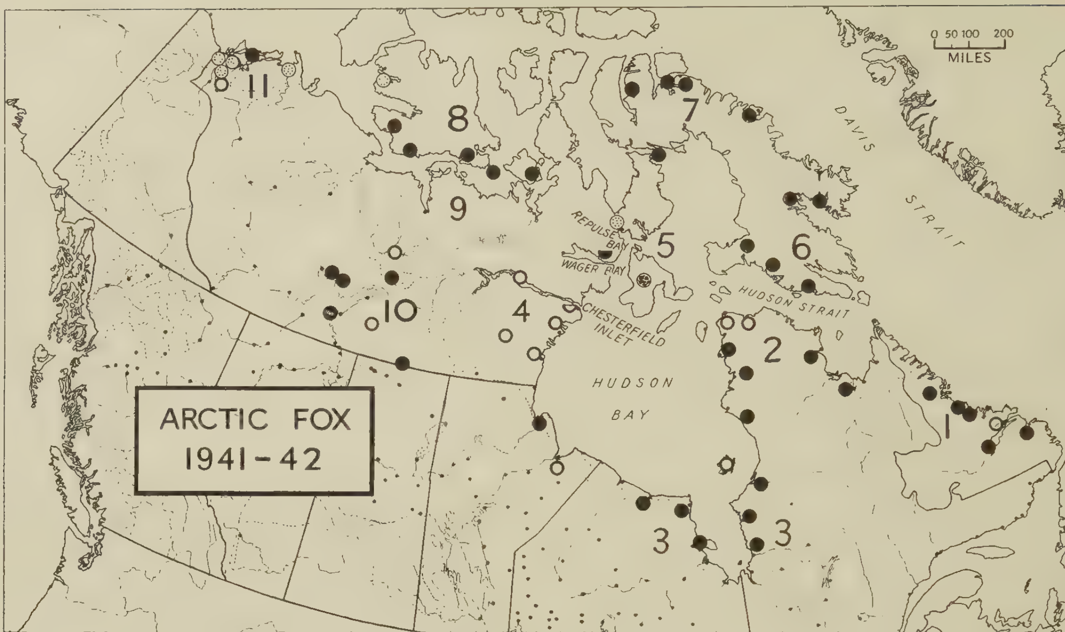

Fig. 1. Reports about the arctic fox population in 1941–42 compared with 1940–41. Each symbol is at the approximate centre of one observer's area: solid black disks are INCREASE; plain circles DECREASE; circles with small dots NO CHANGE, NOT ABUNDANT; circles with larger, irregular dots, NO CHANGE, ABUNDANT. Other black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. (The two semi-circles show reports by one observer for two separate areas.)

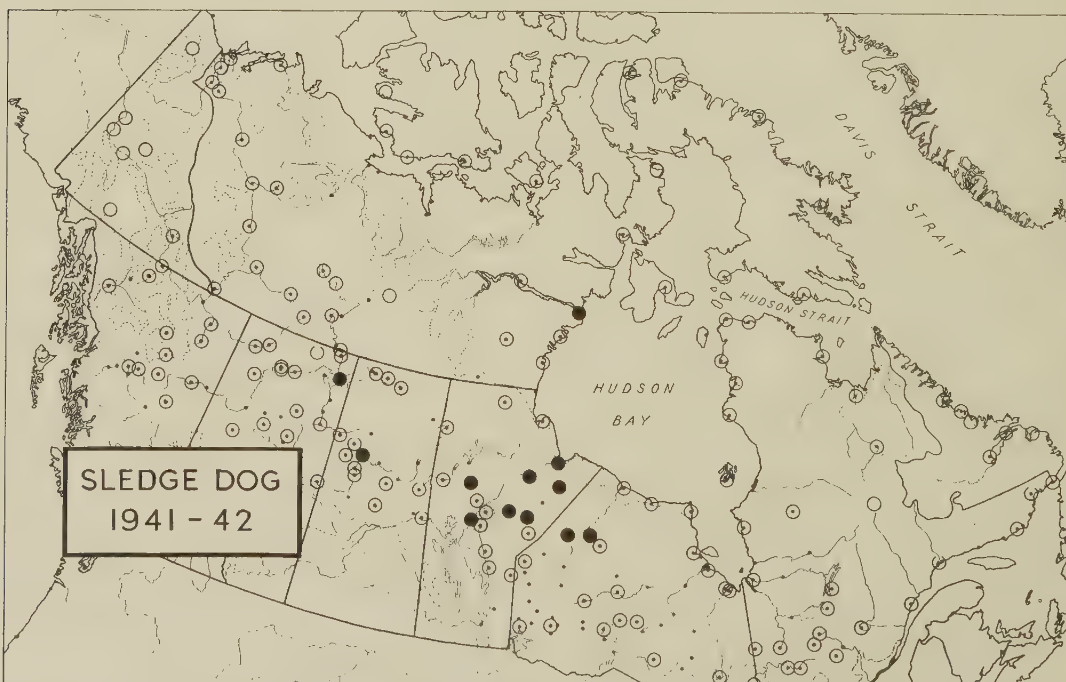

Fig. 2. Prevalence of disease among sledge dogs in 1941–42. Reports of disease, mostly serious, are shown by solid black disks; disease entirely absent by plain circles; other reports by broken circles.

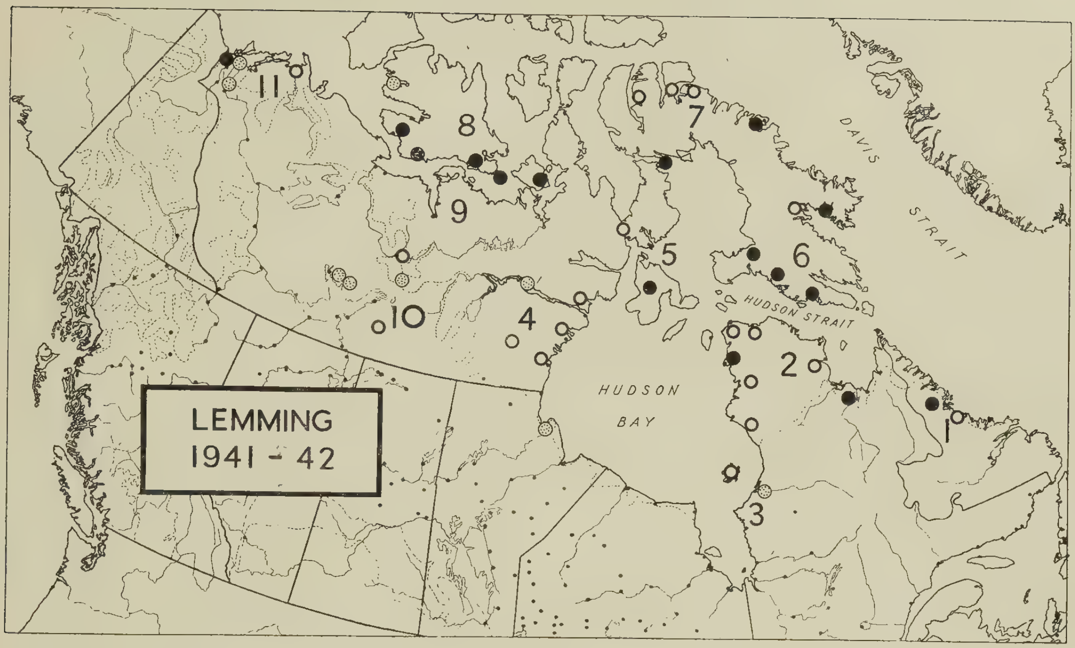

Fig. 3.

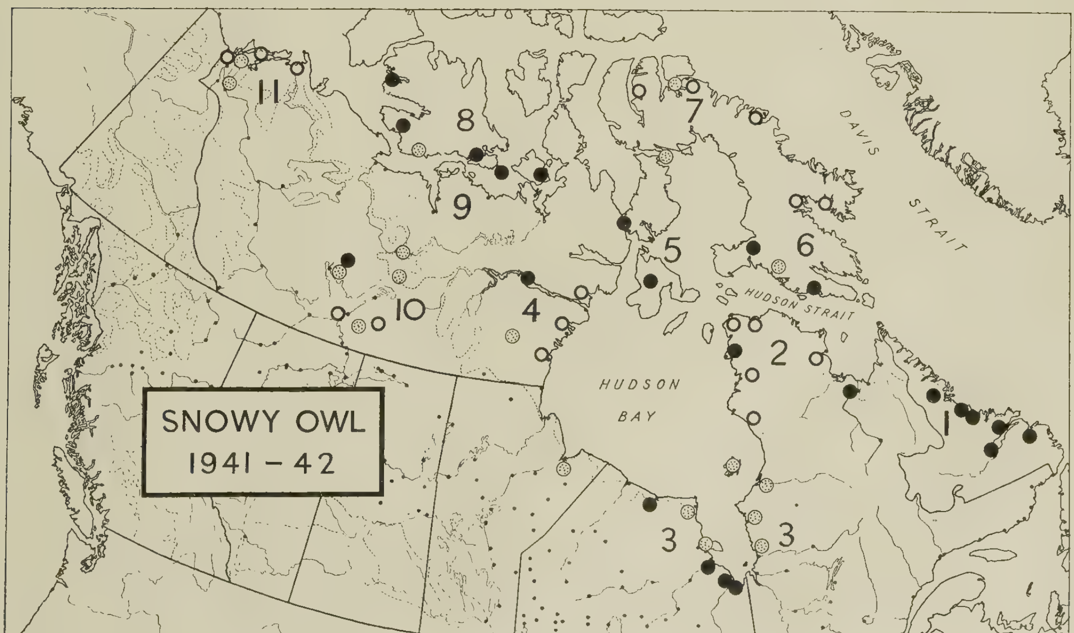

Fig. 4.

Figs. 3, 4. Reports about the lemming and snowy owl populations in 1941–42 compared with 1940–41. Symbols as in Fig. 1.

quite a few white foxes. Run reached its peak in late December. Natives claim there should be another run of foxes this coming winter but not as many as this past winter.' (R. K. Muir.)

2. Northern Quebec and Baffin Island were experiencing their second year of recovery following two poor years (1938–40). Even at Sugluk and Wolstenholme, shown as *decrease* on the map, there had been an abundance of foxes at some time during the season. However, there are indications in some of the following reports that the peak may have been passed by the spring of 1942, especially in those localities where lemming had already gone.

Payne Bay. 'The answers to the fox questions apply only from June to December when both whites and coloureds were very exceptionally abundant at the coast. They hunted on the beaches and could be seen on all the islands and reefs in the bay. Owls were plentiful up to September but then disappeared completely. Lemming disappeared early in summer.' (L. Coates.)

Sugluk. 'White fox were very plentiful in the early fall here but from the first of November on they appeared to migrate southwards; returning during the latter part of April.'

Wolstenholme. 'White foxes were evidently migrating last fall. During October and November they were constantly passing all along the coast from east to west, followed, apparently, by coloured foxes which were preying on them.' (F. Melton.)

Povungnetuk. 'White foxes in great numbers migrated southwards, arriving in this locality about October 5th. They stopped here until after Christmas, then began migrating southwards on the ice. Their numbers must have been considerably depleted by extreme cannibalism amongst them; both white and coloured foxes were culprits and victims.' (R. Cruickshank.)

Pangnirtung. 'A decided increase in fox and lemming signs occurred late April and early May 1941. A decrease noted in these two months of present year 1942.' (J. A. Thom.)

Clyde River. 'From January 1st, 1942 to April 1st, 1942 Eglington Fiord natives north to Scotts Inlet reported complete absence of foxes, while at the same time Home Bay natives reported slight increase which was maintained till early April. Since mid-April numbers seem to have evened out all along the coast with reports of fair signs from all points. As soon as ice made (early November 1941) migration observed of foxes to the west mostly following fresh or nearly fresh bear tracks. Bears scarce all along the coast, presumably owing to complete absence of old heavy ice along coast.' (J. G. Cormack.)

Pond Inlet. 'White fox during September, October and part of November were absolutely numerous in this vicinity, but just before the opening of the season (15th November) they practically all disappeared, and up to the end of the trapping season they did not return in any great number. The natives here are of the opinion that these foxes migrated southward just after the first ice formed. Seals during the outfit were quite plentiful, but lemmings and white owls were very scarce during the latter part of the outfit.' (A. T. Swaffield.)

3. *Pond Inlet*. 'Foxes were very abundant in the early fall, October and until the first week of November when they seemed to migrate south. They were scarce in Navy Board Inlet after the second week of November and remained so all winter. Navy Board Inlet is the only district which showed a decrease from last year. All other districts more numerous.' (J. W. Doyle.)

Arctic Bay. 'During November signs were such that white fox were expected to be more numerous than in Outfit 271. These signs were apparent all over the area in question. During the month of December however, directly after trapping had commenced fox signs were very scarce. Natives maintain that foxes moved south commencing middle of November.' (T. Ross.)

1941–42 was also the second year of increase for foxes, lemmings and snowy owls on King William and Victoria Islands.

King William Island. 'Natives report having noted travelling lemming far out on the sea ice between the mainland and King William Island. They also noted many dead lemming lying on the surface of the snow. Again numerous dead lemming noted in the vicinity of the post towards the end of June when snow commenced to melt.' (L. A. Learmouth.)

7. *Cambridge Bay*. 'Arctic fox seem to be very abundant east of Johnson Point in the Queen Maud Gulf to King William Island, and they were observed to be using fox holes on King William Island by police patrol that passed through that area in early May. (King William Island referred to coast from Tullock Point to Terror Bay.)' (D. C. Martin.)

Read Island. 'White foxes were abundant all outfit. At the end of October there were many signs on the coast, but during first week of November they all migrated inland to about sixty miles from shore and stayed inland all winter and spring and up to the present date they are still there. Though lemming have been plentiful on the coast the foxes seem to prefer to stay inland. Though an abundance of fox food on the land the foxes were not very fat. Their pelts were in excellent condition and very few rubbed or poor skins. It is suggested that in a fairly mild and blizzardless winter as this just past foxes are able to keep in better shape and health which shows finally in the good grade of their skins. A very heavy snow fall in October helped to keep the lemming in this vicinity and the foxes stayed too. After Christmas foxes refused to take bait and were hard to catch. Usually towards the end of March they take bait but this year was an exception. It is noticed here that because the prevailing wind is east no foxes migrate from the west to this vicinity. A fair wind from the west usually brings foxes from the east but an easterly wind takes them away.

'Lemming and mice have been abundant the whole outfit. Lemming were observed on sea ice nearly every month during winter and then again during this month, May, but it is difficult to say whether they were migrating as all their tracks ran in circles. Most of the lemming and their tracks were seen close to shore—about 50 yards or so off the beach, but in May lemmings were seen ten miles off shore on salt ice.' (W. F. Joss.)

Little can be said about any of the 1941–42 population changes on the mainland in the Western Arctic as reports were too few; but there seems to have been a second year of increase in foxes around Great Slave Lake.

Yellowknife. 'Heavy snowfall during the past winter created a condition unknown in this district. White fox was found in the upper part of the Yellowknife River district and also in the Yellowknife Bay district for the

first time to the knowledge of residents, January and February 1942.' (C. W. Snyder.)

3. For the third season foxes were reported increasing or abundant in group 5:

Repulse Bay. 'Fox very scarce on the land but good trapping on the ice and floe edge.' (T. Crawford.)
Southampton Island. 'White fox no change in abundance to last year. Instead of one-year peak fur hunt Southampton always has a two-year peak. Seasons 1940–41 and 1941–42 the same within a few pelts.' (C. Russell.)

Along the west coast of Hudson Bay the fox population had fluctuated from 100% decrease reported in 1939–40 through 100% increase in 1940–41 to 82% decrease in 1941–42. This was the only region in the eastern Arctic to report general decrease in foxes.

Padley. 'Fox plentiful in October and part of November then scarce all winter.' (D. Drysdale.)
12. *Chesterfield Inlet.* 'In the vicinity of Chesterfield Inlet arctic fox was plentiful in early fall. In October and first part of November they seemed to be moving to the westward. This animal was less abundant all along the coast south of Wager Bay to Eskimo Point, but in Wager Bay and around Repulse Bay they were more abundant than last year.' (L. E. Corey.)

(c) *Snowy owl*

With the disappearance of lemmings from most of northern Quebec, northernmost Baffin Island and the west coast of Hudson Bay there was a correlated decrease in snowy owls, or else they were reported gone before the lemmings. However, on the south coast of Baffin Island, also at Fort Chimo and, for part of the year, at Cape Smith, both species increased. In Northern Labrador and the southern part of James Bay snowy owls had also increased; and this links up with the 1941–42 snowy owl migration (Snyder, 1943), the first recorded by the committee established in 1938 to study these periodic flights into southern Canada and the United States. The flight began in the autumn of 1941 and concentrations of owls were reported south from James Bay to the Great Lakes, down the length of the St Lawrence valley and the New England coast.

Owls were still abundant on Southampton Island where lemmings were still on the increase, but at Repulse Bay, where lemmings had decreased, they were plentiful only until the end of January when they practically disappeared. On Victoria Island there was a second year of recovery, and increase was reported from King William Island as well.

3. SLEDGE DOGS

There were only two reports of disease among sledge dogs in the Arctic and Subarctic: at Chesterfield Inlet and York Factory. The latter was probably part of an outbreak affecting many of the posts inland in north-eastern Manitoba and north-western Ontario.

4. SUMMARY

1. Sixty-seven answers were received to questionnaires on population trends during 1941–42 of lemmings (*Lemmus* and *Dicrostonyx*), arctic foxes (*Alopex lagopus*) and snowy owls (*Nyctea nyctea*) in the Canadian Arctic.

2. Arctic foxes were increasing or abundant almost everywhere throughout the Arctic and Subarctic except for the west coast of Hudson Bay where they had crashed after a peak year in 1940–41.

3. 1941–42 was the first year of recovery in arctic fox on the Northern Labrador coast, and around James Bay and the south part of Hudson Bay; for northern Quebec and Baffin Island it was the second year and also for Victoria Island (where lemmings and snowy owls were still increasing); while for Repulse Bay and Southampton Island it was the third year of increase.

4. Lemmings had mostly decreased in northern Quebec and the far north of Baffin Island although they were still abundant farther south in Baffin Island. They had crashed on the west coast of Hudson Bay along with foxes and snowy owls.

5. 'Mice' were more abundant along the Northern Labrador coast and around the southern part of Hudson Bay and James Bay.

6. Snowy owls had disappeared from much of the Eastern Arctic, except for some of the places, particularly Northern Labrador, where there were still numbers of lemmings or 'mice'. There had been a flight into Southern Canada and the United States in the autumn of 1941.

7. Sledge dogs were generally free from epidemics although an outbreak of 'distemper' was reported in north-eastern Manitoba and north-western Ontario.

5. ACKNOWLEDGEMENTS

This is the seventh report of a series based on questionnaires sent out by the Northwest Territories Administration, Ottawa and the Hudson's Bay Company, Winnipeg. Sixty-seven replies dealt with lemmings, arctic foxes or snowy owls: thirteen were received through the Northwest Territories Administration and fifty-four through the Hudson's Bay Company. Other reports dealt with sledge dogs.

Once again we are indebted to the observers who have sent in information and to those who have arranged for collecting and forwarding it to the Bureau of Animal Population, whose work has been financed by the Hudson's Bay Company, and by the Carnegie Corporation of New York through the Carnegie Institution of Washington.

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APPENDICES

Table 1. *Summary of observers' statements about arctic fox, lemming, 'mice', snowy owl and sledge dog (part) for* 1941–42

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, a. = abundant, × = neither.

Sledge dogs: o = disease reported absent. o* = slight disease or starvation reported, + = more serious disease; details in Table 3.

Square brackets indicate observations that have been partly or entirely omitted from map or Table 2: (1) parts or all of some areas are not mapped if they are certainly outside the animal's range; (2) in groups 2 and 3 reports from inland posts are not mapped or included in Table 2; (3) reports on 'mice' and events at special times of the year are not included in the maps or Table 2.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Group 1. Northern Labrador coast					
	Cartwright, half-way both to Frenchman's Island and Rigolet and inland 80 miles. (R. M. Howell)	I. ×	—	N. a.	I. ×	o
	Rigolet, south 50, north 75, west 35 miles. (G. Budgell)	D. s.	none	I. ×	I. ×	o
	Northwest River [and inland 500 miles]. (R. G. Gillard)	I. ×	—	I. ×	I. ×	o
	Hopedale and 30 miles radius. (S. E. Dawe) ...	I. ×	—	N. ×	I. a.	o
	Davis Inlet and 30 miles radius. (W. R. Bull) ...	I. a.	D. ×	N. ×	I. ×	o
	Nain, north 35, south 30 miles; west and northwest 75 miles; coastal islands. (J. F. Delaney) ...	I. ×	I. ×	I. ×	I. ×	o
	Group 2. Coast of Northern Quebec, south to Richmond Gulf [and inland]					
(19)	Fort Chimo to Leaf River and Whale River and inland 60 miles. (S. J. Stewart)	I. ×	I. ×	I. ×	I. ×	o
	[Fort McKenzie, south 150 miles, west 75 miles, north 100 miles, east to Labrador.] (B. J. Soper)	I. ×	I. ×	I. a.	D. s.	o
	Payne Bay to Cape Hopes Advance and Burgoyne Bay; south from Payne River to Leaf Bay. (L. Coates)	I. a.	D. s.	D. ×	D. s.	o
	Summer	—	—	—	[a.]	o
	After December	[s.]	—	—	—	—
	Sugluk, Wakeham Bay to Kovik River [and radius of 100 miles inland]	D. ×	D. s.	—	D. s.	o
	Early fall	[a.]	—	—	—	—
	Wolstenholme; east to within 20 miles of Sugluk, south 70 miles to Kovik River. (F. Melton) ...	D. ×	D. s.	D.	D. s.	o
	October, November	[a.]	—	—	—	—
	Cape Smith; Island, and mainland north to Kovik Bay, south to Magnet Point, inland 50 miles. (P. K. C. Nichols)	I. a.	I. a.	N. s.	I. a.	o
	Winter and Spring	—	[D. s.]	—	[D. s.]	—
	Povungnetuk north to Magnet Point, south to Mistake Bay [inland to Long. 75°]. (R. Cruickshank)	I. a.	D. s.	D. s.	D. s.	o
	Port Harrison, north to Kokiak River, south to Nastapoka Sound [inland to height of land]. (A. B. Fraser)	I. a.	D. ×	D. s.	D ×	o

Table 1 (*continued*)

No.	Locality (observer)	Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Group 3. South parts of Hudson Bay, James Bay [and inland]					
	Belcher Islands. (R. Jeffrey)	D.	D. s.	—	N. s.	o
	Great Whale River, north to Richmond Gulf, south to Cape Jones [inland 100 miles]. (R. K. Muir)	I. a.	N. s.	I. ×	N. ×	o
	Fort George, north 100 miles to Rogan River, south 50 miles to Comb Hills. (R. M. Duncan)	I. ×	—	N. a.	N. s.	o
	[Kanaapuscow and 30 miles radius.] (J. Berezink)	[I. ×]	—	N. ×	[N. s.]	—
	[Nitchequon, north and north-east 50–75 sq. miles.] (T. A. Hambling)	[I. a.]	[I. a.]	—	[N. ×]	—
	Eastmain, Lat. 52–54° [inland to Long. 76°.] (D. G. Boyd)	I. ×	[N. ×]	N. s.	N. s.	—
	Moose Factory and 40 miles radius. (W. M. Watt)	none	none	N. ×	I. s.	o
	Moosonee and 60 miles radius. (C. Thompson)...	none	none	N. ×	I. s.	o
	Albany, 50 miles each side of Albany River [inland 100 miles]. (W. B. Anderson)	none	none	N. a.	I. a.	o
	Attawpiskat, south to the Lawashi River, north to the Ekwan River [inland 150 miles]. Also Agamiski Island. (A. W. Michell)	I. ×	—	I. a.	N. ×	o
	Lake River and 75 miles radius. (K. M. Retallack)	I. ×	—	I. a.	N. s.	o
	Weenusk, north 70, south 50, inland on Weenusk River [150 miles]. (J. Mathieson)	I. ×	—	I. a.	I. ×	o
	York Factory and 100 miles radius. (H. F. Blane)	D. s.	none	s.	N. ×	+
	Group 4. West coast of Hudson Bay, north from Nelson River and inland					
	Churchill to Cape Churchill [north to Long Point], and inland 50 miles. (A. B. Urquhart)	I.	N.	N.	none	o
	Eskimo Point, south to Nonala, west to Padley, including Maguse Lake area. (W. C. Brownie)...	D. ×	D. s.	D. s.	D. s.	o
	{Padley and 50 miles radius. (D. Drysdale) ...	D. s.	D. s.	D. s.	N. s.	o
	{*October, November*	[a.]	—	—	—	—
(13)	{Tavane, north to Rankin Inlet then west to Kaminuriak Lake, then south to Maguse Lake, then east along Maguse River to coast and north to Tavane. (G. Anderson)	D. s.	D. s.	—	D. s.	—
	{*April* 1942	[I.]	—	—	—	—
12.	Chesterfield Inlet, south to Eskimo Point, north to Repulse Bay, including shores of Wager Bay. (For fox, Wager Bay and north: I. (group 5); south of Wager Bay: D. (but abundant in fall). * (L. E. Corey)	{I. {D. ×	D. ×	—	D. s.	+
	Baker Lake vicinity. (A. Lunan)	D. ×	N. ×	—	I. ×	o
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
	{Repulse Bay, east to Lyon Inlet, west to Pelly Bay, north to half-way up east coast of Committee Bay, and (group 4) south to Bury Cove. (T. Crawford)	N. ×	D. ×	—	I. ×	o
	{*After January*	—	—	—	[D. s.]	—
	{On the ice	[a.]	—	—	—	—
(4)	Southampton Island. (C. Russell)	N. a.	I. a.	—	I. ×	o
	Group 6. Southern Baffin Island					
	Lake Harbour from Robinson Sound and Frobisher Bay to south coast of Baffin Island, west to Markham Bay. (R. H. Kilgour)...	I. a.	I. a.	—	I. ×	o
11.	Lake Harbour, Cape Dorset and Frobisher Bay districts. (H. O. Humphrey)	I. a.	I. a.	—	N. ×	o
	Cape Dorset and Foxe Peninsula south and west of Koukdjuak River, Nettiling Lake, Amadjuak River and Lake and Mingo Lake. (O. M. Demment)	I. a.	I. a.	—	I. ×	o

* Observer's vote is halved (Table 2).

Table 1 (*continued*)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Pangnirtung. Cumberland Sound and 30 miles inland. (J. A. Thom)	I. a.	D.	—	D.	o
	April, May	[D.]	—	—	—	—
2.	Pangnirtung Fiord. (R. W. Hamilton)	I. a.	I. a.	—	D. s.	o
	Group 7. Northern Baffin Island, and north. Also Igloolik					
	Clyde River to Coutts Inlet and Home Bay. (J. G. Cormack)	I. ×	I. ×	—	D. s.	o
	Eglington Fiord to Scotts Inlet, 1 *January to* 1 *April*	none	—	—	—	—
	Pond Inlet, Eclipse Sound, Navy Board Inlet and south-east to Coutts Inlet. (A. T. Swaffield) ...	I. ×	D. ×	—	N. s.	o
	November	[s.]	[s.]	—	[s.]	—
3.	Pond Inlet, Eclipse Sound, Tay Sound, Milne Inlet, Bylot Island, Navy Board Inlet and south-east to Clyde River. (J. W. Doyle)	I. ×	D. s.	—	D. s.	o
	Navy Board Inlet, *winter*	[s.]	—	—	—	—
	Igloolik; Melville Peninsula north of Amitok Peninsula and Garry Bay, coastal strip east from Gifford Fjord, islands in north Foxe Basin. (J. M. Stanners)	I. a.	I. ×	—	N. s.	o
	Arctic Bay, all of Admiralty Inlet and Bernier and Agu Bays. (T. Ross)	I. ×	D. s.	—	D. s.	o
	Group 8. Boothia Peninsula and Islands west and north					
(5)	King William Island and (group 9) mainland south to Backs River. (L. A. Learmouth) ...	I. a.	I. a.	—	I. a.	o
	Cambridge Bay and 50 miles radius (probably includes group 9). (E. J. Gall)	I. ×	I. ×	none	I. ×	o
	January to May	[a.]	[a.]	—	[×]	[o]
7.	Cambridge Bay, Victoria Island vicinity and to Tullock Point, King William Island. (D. C. Martin)	I. a.	I. a.	—	I. ×	o
	West of Johnson Point, *middle of February* ...	[D. s.]	—	—	—	—
26.	Richardson Island, coast from Lady Franklin Point to Byron Bay, Victoria Island and inland 50 miles. (O. Andreasen)	I. a.	N. a.	—	N. s.	o
	Read Island; Lady Franklin Point, west along coast to Cape Baring, east to extreme east end of Prince Albert Sound, back overland. (W. F. Joss) ...	I. a.	I. a.	—	I. ×	o
(8)	Holman Island from Investigator Island in Prince Albert Sound to Minto Inlet and Deans Dundas Bay. (F. R. Ross)	N. ×	N. ×	—	I. ×	o
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Fond du Lac: north 150 miles towards Wholdaia Lake. (L. A. Martin)	I. a.	—	D. ×	—	o
27.	Fort Fitzgerald, north-east 250 miles north 100 miles [west 150 miles]. (J. W. Nichols) ...	D. ×	D. s.	—	D. s.	o
	Fort Resolution and 50 miles radius	I. s.	—	I. a.	D. s.	—
	Rocher River, east 100 miles and south [100] miles. (A. Stewart)	none	none	N. ×	N. s.	—
	Snowdrift, north and east into barren lands. (S. P. Hume)	I. a.	N. ×	I. a.	N. ×	—
29.	Fort Reliance, north of west end of Aylmer Lake to Icy River. (G. Magrum)	D. a.	D. ×	—	N. ×	o
	Fort Rae, south-east 80, north and north-east 150 [north-west 150 and north-north-west 180 miles]. (R. Middleton)	—	—	I. a.	I. a.	o
	Yellowknife; Lat. 62–63°, Long. 112–116°. (A. Reid)	I. a.	N. ×	N. ×	none	—
16.	Yellowknife Bay and River. (C. W. Snyder) ...	I. a.	N. ×	—	N. ×	o

Table 1 (*continued*)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Group 11. Coppermine River to Alaska					
9.	Liverpool Bay, west to Cape Dalhousie, north-east to Baillie Island. (S. Mason)	N. ×	D. s.	—	D. s.	o
	Tuktuk, north to Baillie Island, east to east side of Huskie Lakes, west to west side of Richards Island, south to Kittigazuit	I. ×	—	I. a.	D. s.	—
(14).	Arctic Red River and radius of 50 miles. (L. Roy)	—	—	I. a.	—	o
30.	Arctic Red River to Aklavik: to Thunder River [and 100 miles further up Mackenzie River; 35 miles west]. (J. E. Nagle)	D. ×	N. s.	—	N. ×	o
	Aklavik, Mackenzie River Delta. (C. Reiach) ...	N. ×	none	N. ×	none	o
17.	Mackenzie River Delta. (L. Weston)	N. ×	N. ×	—	N. ×	o
20.	Aklavik Reindeer Reserve and Mackenzie River Delta. (J. A. Parsons)	N. ×	I. a.	—	D. s.	o

Table 2. *State of the arctic fox, lemming and snowy owl populations in* 1941–42. *Number of observers reporting relative abundance compared with* 1940–41

	Eastern Arctic									Western Arctic					
Group no. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	5	5	6	1	½	5	5	27½	**71**	5	.	5	1	11	**58**
Decrease	1	2	2	4½	.	.	.	9½	**24**	.	.	2	1	3	**16**
No change	.	.	.	.	2	.	.	2	**5**	1	.	.	4	5	**26**
Total	6	7	8	5½	2½	5	5	39	**100**	6	.	7	6	19	**100**
Lemming:															
Increase	1	2	.	.	1	4	2	10	**35**	4	.	.	1	5	**33**
Decrease	1	5	1	4	1	1	3	16	**55**	.	.	2	1	3	**20**
No change	.	.	1	2	.	.	.	3	**10**	2	.	3	2	7	**47**
Total	2	7	2	6	2	5	5	29	**100**	6	.	5	4	15	**100**
Snowy owl:															
Increase	6	2	4	1	2	2	.	17	**41**	5	.	1	.	6	**33**
Decrease	.	5	.	3	.	2	3	13	**32**	.	.	2	3	5	**28**
No change	.	.	7	1	.	1	2	11	**27**	1	.	4	2	7	**39**
Total	6	7	11	5	2	5	5	41	**100**	6	.	7	5	18	**100**

Table 3. *Information about sledge dogs*, 1941–42

All replies in the following table were received from the Hudson's Bay Company. Reports of serious disease are marked + in this table and shown by a black disk on the map. Outbreaks apparently less serious, deaths through starvation, etc. are shown by a broken circle on the map. Absence of trouble is shown by a full circle; but names of these posts, other than those given in Table 1, are not listed. Fuller descriptions of some of the areas are in Table 1.

Quebec

St Augustine. 'Very little disease in this outfit, the same as last year but not so pronounced. Origin was the same as last year and symptoms were similar but not so pronounced. About 12 to 20 dogs were affected and not more than six died. No treatment.' (B.G.C.)

Seven Islands. 'Dog disease seems to be permanent among dogs here, with cases intermittently every year. Symptoms were collapse of hindquarters, internal pain, discharge from nose. Number affected unknown.' (G.A.S.)

Ontario

\+ *Bearskin Lake.* 'Disease began in April, origin unknown. Symptoms were bad cough and discharge at the nose. Around forty dogs were affected and ten died. They were treated with castor oil only.' (W.J.H.)

\+ *Trout Lake.* 'Disease began in April, spreading from Bearskin Lake. All we noticed was a tendency on the part of the dogs to head for water, seemed very thirsty. Discharge from eyes and nose. Thirty dogs were affected, all died. No treatment was attempted.'

Table 3 (*continued*)

Manitoba

\+ *Rossville.* 'Disease began in March, origin unknown. Symptoms were distemper, nose and eyes running pus. Under 50 dogs were affected, but most of these died. Treatment was attempted in only a very few cases.' (T.F.)

\+ *God's Lake.* 'Disease began about April 1, origin unknown. Symptoms were distemper, affecting nearly all pups and about 10 % of older dogs. It killed more than 30 % of the pups, the biggest and healthiest. Of the older dogs it attacked only those in poor condition. I do not know how many died. No distemper among our old dogs. only Indian dogs. We gave distemper pills to pups and lost one out of four.' (J.L.C.)

\+ *Oxford House.* 'Disease began in January, origin unknown. Symptoms resembled a cold in a human being. Dogs would not eat and gradually grew weaker. Estimate 60 % of all dogs were affected, 90 % of which died. Sick dogs were isolated, kept warm and given a strong dose of Epsom Salts. Not very effective. Any dogs that recovered seemed to be affected by twitchings of their heads and bodies.' (D.D.)

\+ *Shamattawa.* 'Disease began in January, origin unknown. Disease believed to be distemper. About 75 or more dogs were affected and about 50 died. Laxatives were given.' (F.G.F.)

\+ *Gillam.* Disease began in January, origin unknown. Symptoms were paralysis of the hindquarters and loss of appetite. Practically all the dogs were affected, about 100 died. Spratts Distemper Pills were given. This did very little good if animal had been sick a few days before treatment given. If given at once animal recovered in most cases.' (E.J.H.)

Split Lake. 'A little north of here and at "Line", disease believed to be distemper broke out from February to April. Not many dogs affected yet and no treatment given.' (A.G.M.)

\+ *Nelson House.* 'Disease occurred in November with symptoms of paralysis. Dogs ate carcass of horse which had sleeping sickness. 50 or 60 were affected and 90 % died. No treatment was attempted.' (E.J.S.G.)

Saskatchewan

Cumberland House. 'Disease occurred in December, origin unknown. Symptoms resembled dropsy. Approximately 12 dogs were affected, five died. No treatment attempted as sickness unknown.' (F.R.)

Pelican Narrows. 'Disease carried through from previous outfits, origin was fish liver flukes and distemper imported from Flin Flon. Symptoms were lassitude and debility. Intestinal cavity filled with clear liquid, green tinge throughout liver which was covered with small yellow spots containing pus. Number affected unknown. (A.H.)

\+ *Pine River.* 'Disease occurred in July and August, origin unknown. Dogs seemed ailing a while and in many cases wandered away to die. Approximately 75 were affected and 50 died. No proper treatment.' (A.A.)

Clear Lake. 'Disease, believed to be distemper, occurred in April. Origin unknown. About 6 % were affected and six died. Treatment was attempted.' (P.M.P.)

Alberta

\+ *Fort Chipewyan.* 'Disease began in November, appeared to come from Jackfish River and might have been caught through the fish eaten by the dogs there. Dogs were quite happy but suddenly quit eating and died in about 2 days, thought to have been distemper. About 35 dogs were affected, of which 20 died. No treatment was attempted.' (W.M.S.)

Wood Buffalo Park. 'Disease occurred in March and April. Seemed to be a mild form of distemper; indicated first by coughing, later pus in eyes. Of 12 dogs affected two died. Those dogs which were laid off from work immediately recovered with the exception of one six-month pup. Treatment: dosed for worms, castor oil, isolated, given warm dry quarters.' (M.J.D.)

Hudson Bay and Inland

\+ *York Factory.* 'Disease began in February, origin unknown. Symptoms were weakness of back and legs, dogs walking around without control of back legs. Roughly 20 were affected, nearly all died. No treatment was attempted.' (H.F.B.)

\+ *Chesterfield Inlet.* 'Disease occurred in May, June and July, coming from the south. First there was a lack of appetite, followed by a discharge of pus from the eyes and nose, accompanied in some cases by lassitude and in some instances diarrhoea. Some of the dogs had convulsions, in others a sort of twitching of the ears and eyelids was noticed. Some of the dogs died after a few days' sickness, while others lived for a longer period. Death resulted in the majority of cases, bitches being less susceptible than males. 50 % mortality in the whole district.' (L.E.C.)

THE BREEDING DISTRIBUTION, HISTORY AND POPULATION OF THE NORTH ATLANTIC GANNET (*SULA BASSANA*)

PART 1. A HISTORY OF THE GANNET'S COLONIES, AND THE CENSUS IN 1939

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(With Plates 1–10 and 5 Figures in the Text)

CONTENTS

1. INTRODUCTION

(*a*) Objects of this paper

In 1939 an attempt to make a census, within the space of one breeding season, of the world population of the gannet (*Sula bassana* L.), was organized by the writers. Twenty-seven observers took part, and were asked to visit the known colonies of this bird and make accurate counts of the number of breeding pairs. It was intended that each colony should be visited by one or more ornithologists who had had previous experience in visiting gannet colonies, and in counting the number of occupied nests.

The objects of this paper are to give an account of the success of this undertaking; to set out what the writers have learned from a search of the existing literature (which has occupied much of their spare time during the last seven years) about the history of the gannet's colonies; to reach conclusions about trends in the gannet's population during the last hundred years; and to discuss certain ecological points, and biological matters, which arise from this survey.

Part 1 of this paper is devoted to the results of the census and the accounts of the history of each of the colonies. Part 2 will contain the general conclusions about population trends, and the ecological discussion; it will contain few facts about the gannet which are not published in Part 1.

It must be recorded that our interest in the gannet has been largely aroused, and wholly maintained, by the beauty of this great sea-bird, and the romance of its surroundings. It is, moreover, undeniable that the aesthetic delight of observing gannets has accounted for the enthusiasm of our co-operators, and the ease with which we were able to persuade them so to become.

(*b*) The world population of individual species of animals

There are extremely few animals of which the world population is at all accurately known. Mostly, these are animals which have undergone preservation as domestic or semi-domestic species; or conservation as wild or semi-wild species, or as animals of economic importance. Of all the species of animals which cannot be regarded as rare, we can only find world figures, of any accuracy, for four. Among the rare forms, we can only find good figures for three species and one subspecies, and estimates of varying degrees of reliability for a handful of others. It is surprising how little has been investigated in this field; it is possible to think of many species of which a world census would appear possible—but has not, as yet, appeared practicable to anybody. It is suggested that the following lists, in descending order of numbers, constitute a large sample of existing world census figures:

Counts and estimates of some accuracy, species

Man, *Homo sapiens* L., *c.* 2000×10^6; estimate 1940 (243).

Fur seal, *Callorhinus alascanus* (Jordan & Clark), 3 populations: Pribilof islands 1,839,119, 1937; 2,185,136,

1940 (**35**, **102***a*); total all ages, economically valuable, heavily conserved, wild: Commander islands, 40,000 (commentary to film 'One day in the life of the Soviet Union', Moscow, 1941), heavily conserved: Robben island, Kuriles, 'something over 11,000', 1918 (**102***a*); this is last available information about this colony, which is heavily, and very secretly, conserved. World total probably *c.* 2¼ million.

Gannet, *Sula bassana* L., 165,600; breeding adults 1939 (present paper). Slight economic value, partly conserved, wild.

American bison, *Bison bison* (L.), 14,445, 1924; 21,701, 1933 (**81***a*, **200**); past economic value, all conserved, semi-wild.

Père David's deer, *Elaphurus davidianus* A. Milne-Edw., *c.* 200, 1940 (**287**); no present economic value, all at Woburn Park, Bedfordshire, England.

European bison, *Bison bonasus* (L.), 97 on 1 January 1938 (**251**); no present economic value, all in zoos and parks.

Ivory-billed woodpecker, *Campephilus principalis* (L.), *c.* 24, 1939 (**219**, **220**); no economic value, partly conserved, wild.

Count of some accuracy, subspecies

St Kilda wren, *Troglodytes troglodytes hirtensis* Seeb., 136 breeding adults 1931 (**101**); about the same number 1939 (**174**); conserved, wild.

Counts and estimates of unknown accuracy, species

Atlantic grey seal, *Halichoerus grypus* (Fab.), *c.* 10,000 (**57**); economic value, partly conserved, wild.

Indo-Chinese forest ox, *Novibos sauveli* (Urbain), *c.* 1000, 1939 (**52***a*); wild, only known since 1930.

Trumpeter swan, *Cygnus buccinator* Richardson, *c.* 212–300, 1939–40 (**17**, **46**); no economic value, all save *c.* 16 in reserves.

White-tailed gnu, *Connochaetes gnou* (Zimm.), 'probably not more than a few hundred', 1939 (**29**); partly conserved, some wild, some in captivity.

Great Indian rhinoceros, *Rhinoceros unicornis* L., *c.* 200, 1932 (**107**); economic value (through superstitions concerning horn, urine, etc.), wild, a few in captivity.

Whooping crane, *Grus americana* (L.), probably not more than 200, 1942 (**211***a*); no economic value, slightly conserved, wild.

Javan rhinoceros, *Rhinoceros sondaicus* Desm., *c.* 66, 1937 (**131**); economic value as *R. unicornis*, all wild.

Californian condor, *Gymnogyps californianus* (Shaw & Nodder), *c.* 45, 1938 (**187**); no economic value, partly conserved, all wild save one or two in captivity.

Count and estimates of unknown accuracy, subspecies

Florida wild turkey, *Meleagris gallopavo osceola* Scott, *c.* 12,300, 1939 (**154***a*); economic value, partly conserved, wild.

Great white heron, *Ardea occidentalis occidentalis* Audubon, 600, 1939 (**179**); conserved, wild.

Mountain zebra, *Equus zebra zebra* L., not more than *c.* 100, 1939 (**29**); mostly conserved and in semi- or complete captivity.

Count of some accuracy of majority of population, species

Pronghorn, *Antilocapra americana* Ord, 131,555 in U.S.A. *c.* 1939 (**98***a*); conserved, wild, small unknown population also in Mexico.

(*c*) Previous estimates of the world population of gannets

Sula bassana is restricted to the North Atlantic Ocean, though individuals may penetrate into, though not breed in, the islands of the Canadian Arctic Archipelago (**290**). It has always attracted the attention of naturalists, and is dealt with widely in the literature of all countries bordering on its ocean. It has been the subject of a monograph—J. H. Gurney's 'The Gannet. A Bird with a History' (1913). Gurney was the first to attempt an assessment of the bird's world population, putting it at 101,000 breeding individuals in *c.* 1912. This figure was based on estimates of the population at the colonies then known, made in years between 1887 and 1908.

A much more accurate survey of the world population was that of Wynne-Edwards, Lockley & Salmon (**65**), who based their final figure of 156,000 breeding birds on counts and estimates made between 1928 and 1935, with the exception of one colony which had not been visited since 1914.

(*d*) Methods of estimating and counting the numbers of gannets

A short summary of methods has already been given (**236**). Though some of the earlier estimates of numbers were based on the number of young birds taken by man at various colonies, the basis of nearly all modern counts and estimates is the number of occupied nest-sites in the colony. Methods which have been used in determining this number can be summarized as follows:

1. *Direct*

(*a*) *Direct counts of occupied nests*

(i) *By eye*: this is the most satisfactory method and has been used wherever practicable in the 1939 census.

(ii) *By glasses and telescope*: these instruments have been used to help the counts by eye, for instance, on Ailsa Craig and Noss. Under many conditions their use is not possible, e.g. from a rowing boat (unless there is a flat calm), from the deck of a small ship under sail in rough weather, as at Sule Stack, or from the deck of a boat or ship with the engine running.

(iii) *From photographs*: the method of counting from photographs (which are best accompanied by compass bearings) is extremely useful. It must be regarded, however, as accessory to the method of direct visual counts. It was found very useful for counting Sule Stack, and Grassholm in various years. Perhaps its best use is for comparisons of the population from year to year; such comparisons have been made in the study of the gannetries on Ailsa Craig, Grassholm, Sula Sgeir, St Kilda and Bird Rocks.

The photographic method was (as far as we know)

first applied to the comparison of animal numbers by Jordan & Clark (117), who published, in 1898, a study of changes in the population of fur seals on the Pribilof islands.

(*b*) *Estimation*

(i) *By area*: when weather and time are important factors, it is not always possible to count every nest separately. Thus it was found necessary to estimate certain parts of the St Kilda colony by comparing groups of nests with others that had been previously counted.

(ii) *By the alighting method*: this was first used to estimate parts of the Ailsa Craig population in 1936 (236). The details need not be recapitulated here, but it should be pointed out that we overestimated its accuracy. Although it is useful for determining diurnal activity, and for determining the number of times each bird visits its nest in the day, we decided (particularly after criticism by Malcolm Stewart) to discard the method in taking the 1939 census.

2. *Indirect*

(*a*) *From records of eggs, young and adults taken*

Much of the evidence concerning the past populations of colonies is based on such records. In the present inquiry little use has been found for them, save in tracing the order of magnitude, rather than the absolute population, of a few colonies.

(*b*) *From records of total area occupied*

At several colonies, such as Sula Sgeir, Grassholm and Bird Rocks, visitors have delineated the area occupied by gannets' nests in various years. This has proved useful in tracing, not the actual population, but whether there has been an increase or a decrease.

2. THE GANNET'S COLONIES

(*a*) List of present and past gannet stations

A list of the places where gannets breed, have bred, have been suspected to have bred, or have occupied cliffs or ledges in the breeding season, is as follows:

South-west Britain Group			
Cornwall	1.	Gulland Rock†	50° 34′ N., 4° 59′ W.
Devonshire	2.	Lundy Island*	51° 12′ N., 4° 40′ W.
Pembrokeshire	3.	Grassholm	51° 44′ N., 5° 30′ W.
Caernarvonshire	4.	Great Orme's Head	53° 21′ N., 3° 52′ W.
Kerry	5.	Little Skellig	51° 46′ N., 10° 30′ W.
Cork	6.	Bull Rock	51° 35′ N., 10° 19′ W.
Wexford	7.	Great Saltee	52° 06′ N., 6° 38′ W.
Mayo	8.	Stags of Broadhaven*	54° 22′ N., 9° 47′ W.
East Britain Group			
Yorkshire	9.	Bempton Cliffs	54° 09′ N., 0° 10′ W.
East Lothian	10.	Bass Rock	56° 05′ N., 2° 40′ W.
Fife	11.	Isle of May*	56° 11′ N., 2° 33′ W.
West Britain Group			
Isle of Man	12.	Calf of Man	54° 03′ N., 4° 49′ W.
Wigtownshire	13.	Scar Rocks	54° 40′ N., 4° 42′ W.
Clyde Islands	14.	Ailsa Craig	55° 15′ N., 5° 08′ W.
South Inner Hebrides	15.	Islay†	55° 45′ N., 6° 15′ W.
North Inner Hebrides	16.	Eigg†	56° 53′ N., 6° 08′ W.
	17.	Rum†	57° 00′ N., 6° 20′ W.
North Britain—Faeroes Group			
Outer Hebrides	18.	Oigh-sgeir Eagach (Haskeir)†	57° 42′ N., 7° 42′ W.
	19.	St Kilda	57° 52′ N., 8° 30′ W.
	20.	Rockall	57° 40′ N., 13° 30′ W.
	21.	Sula Sgeir	59° 06′ N., 6° 09′ W.
	22.	North Rona†	59° 07′ N., 5° 49′ W.
Orkney	23.	Sule Stack	59° 02′ N., 4° 30′ W.
	24.	Copinsay*	58° 54′ N., 2° 41′ W.
Shetland	25.	Noss	60° 09′ N., 1° 02′ W.
	26.	Hermaness	60° 51′ N., 0° 54′ W.
Faeroes	27.	Myggenaes Holm	62° 08′ N., 7° 41′ W
Iceland Group			
	28.	Westmann Islands	63° 23′ N., 20° 20′ W.
	29.	Eldey	63° 44′ N., 22° 57′ W.
	30.	Grímsey	66° 32′ N., 18° 00′ W.

* Now extinct. † Of doubtful or vague history.

ST LAWRENCE GROUP		
New Brunswick	31. Gannet Rock, Grand Manan*	44° 34′ N., 66° 46′ W.
Nova Scotia	32. Gannet Rock, Yarmouth*	43° 55′ N., 65° 45′ W.
Quebec	33. Bird Rocks, Magdalen Islands	47° 51′ N., 61° 08′ W.
	34. Bonaventure Island, Gaspé	48° 29′ N., 64° 09′ W.
	35. Perroquet Islands, Mingans*	50° 13′ N., 64° 12′ W.
	36. Gull-cliff Bay, Anticosti Island	49° 11′ N., 54° 11′ W.
Newfoundland	37. Cape St Mary, Avalon Peninsula	46° 49′ N., 54° 11′ W.
	38. Bacalieu Island	48° 60′ N., 52° 47′ W.
	39. Funk Island	49° 47′ N., 53° 12′ W.

* Now extinct.

(*b*) COLONIES VISITED DURING THE SURVEY

Plans for a world census of gannets in 1939 were first made in 1936, after consultation with Messrs Wynne-Edwards, Lockley & Salmon, the organizers of the previous survey. These ornithologists helped us in every way they could, R. M. Lockley visiting Grassholm personally and V. C. Wynne-Edwards providing contacts with observers in the Gulf of St Lawrence area. We are very grateful to them for all they have done.

Preliminary work was made possible by an annual gannet-counting party on Ailsa Craig, which was joined, in one year or another, by many of those who took part in the final survey. Here counting methods were worked out, and the members of the team got plenty of practice.

In 1939 the census parties, and their objectives, were:

J. Buxton and R. M. Lockley	Grassholm
Miss C. M. Acland	Little Skellig
L. P. Madge and H. E. Wall	Bull Rock
E. A. Constable	Great Saltee
A. Gore-Booth and R. F. Ruttledge	Stags of Broadhaven
R. Chislett and M. Stewart	Bempton Cliffs
J. Bain	Bass Rock
K. Williamson	Calf of Man
J. M. McWilliam	Scar Rocks
F. Fraser Darling, J. Fisher, M. Stewart and H. G. Vevers	Ailsa Craig
C. P. Blacker, J. Fisher, J. S. Huxley and E. M. Nicholson	St Kilda and Sule Stack
Above party, R. Atkinson and F. Fraser Darling	Sula Sgeir
Coastal Command, Royal Air Force	Rockall (1941)
J. Fisher and J. S. Huxley	Noss
M. Stewart	Hermaness
L. S. V. Venables and H. G. Vevers	Myggenaes and Eldey
W. G. Alexander, F. C. Evans and H. G. Vevers	Westmann Islands
W. G. Alexander, F. C. Evans, L. S. V. Venables and H. G. Vevers	Grímsey
W. Duval and L. I. Grinnell	Bonaventure
H. F. Lewis	Gull-cliff Bay (1940)
O. J. H. Davies and R. D. Keynes	Cape St Mary

Owing to circumstances beyond their control, Messrs Davies and Keynes were prevented from reaching Funk Island. This colony was last seen in 1937, when 7 pairs were breeding. The 40-year-old colony on Bacalieu Island was not discovered by ornithologists until Peters (**184***a*) found 200 nests there in 1941. Otherwise, the only serious omission in the census was the colony on Bird Rocks, last seen by A. O. Gross in 1934, when there may have been 1000–1500 pairs.

It can be seen that, taking into account the general inaccessibility of gannet colonies, the teams undertook their self-appointed tasks with great success. We are extremely grateful to every member of them. Many of them have endured considerable expense and inconvenience; all have permitted us to use their complete notes and records.

(*c*) SOUTH-WEST BRITAIN GROUP

1. Gulland Rock, Cornwall

William Botoner, who wrote his *Itinerary* in *c.* 1468, mentions gannets as nesting on a rock called Pentybers, which Gurney (**95**) identifies with Gulland Rock, not far from Pentyr Point, north Cornwall. No later record of breeding here has been found, and birds are certainly not present to-day.

Summary

Breeding *c.* 1468; not breeding in recent years.

2. Gannet Stone, Lundy, Devon

We have considered it quite unnecessary to recapitulate Gurney's observations, quotations and references (**95**) unless, as is sometimes the case, they need criticism or correction. Hence we add to Gurney's history of the Lundy colony only such information as he does not publish, and such as has accrued since his time. This new information is then lumped with Gurney's material in the summary. We have done the same thing in our treatment of many of the other colonies that follow.

According to Chanter (**46***a*) it would appear that

Copyright *Fox Photos*

Photo. 1. Gannets nesting on Grassholm, 21 June 1937. In this year there were about 5000 nests on the whole of the island. The typical 'flat-ground' gannet's nest can be seen to be mound-like; it is composed of material gathered in many seasons. Each pair of gannets occupies an area of about 1 square metre.

 R.A.F. official photo

Photo. 2. View of Little Skellig, approximately from the north, 29 July 1941. Highest point *c.* 445 ft. This is the second largest gannet colony in the world, with between 9000 and 10,000 breeding pairs. Reproduced by permission of Coastal Command, Royal Air Force.

 R.A.F. official photo

Photo. 3. Close view of Little Skellig, approximately from the north-west, 29 July 1941. In the background lie Dursey Island, and the Cow and Bull Rocks. Of the 9000–10,000 nests on Little Skellig, over 2800 are visible on the ledges of this part of the rock. Reproduced by permission of Coastal Command, Royal Air Force.

gannets were still 'plentiful' in about 1871, though at that time he writes 'they, as well as the other sea-birds, are perceptibly and rapidly decreasing in numbers, from the incessant and reckless robbery of their nests during the breeding-season, principally by the crews of pilot and tug-boats'. From the account of D'Urban & Mathew (**62**) it would seem that the number of nests in 1890 was about 70. Capt. W. Dark, of Appledore, avers that two birds attempted to build, with no success, in 1905 (**138**). By 1909 the gannet had become entirely extinct on Lundy (**55**).

In 1922 a surprising attempt at recolonization was made (**138**). On 8 May an adult settled on the old Gannet Rock, and it spent most of its time at this spot until 11 May, when it left. On 19 May it returned, started to build on the north side of the rock, but left after continuous fogs, possibly disturbed by the foghorns at the north end. On 24 May it returned and began to build again, but left in early June, after which no more was seen of it.

In 1938 Mr M. C. Harman (**281**) had twenty gannets' eggs sent from Grassholm by Mr R. M. Lockley. He writes: 'the eggs arrived rather late and were put rather lavishly into the cormorants' nests and a few others. I rode up to the north end of the island (on 5 August) and looked through field-glasses at our Gannet Rock. There were two young birds at the top of the rock that I believed were gannets. Others confirmed that view, but it is not certain.' In 1939 Mr Harman reported that the scheme was 'a complete failure again', the cormorants having for the most part thrown out the eggs or deserted them; thus we can also conclude that no young ones were reared in 1938.

Summary

Breeding 1274.

Breeding 1321, 1325 or 1326.

Breeding 1631.

Not mentioned 1787.

Breeding 1829, 1839.

Plentiful but decreasing through persecution 1871.

Persecution continuing; none reared *c.* 1883–*c.* 1891; 16 nests, none reared 1887; nearly 70 nests, none reared 1889.

Eggs taken, *c.* 70 nests, none reared 1890; 30 pairs present 1893.

3 pairs present 1900; 7 pairs present 1901; no report 1902; 5 pairs present, 5 eggs taken 1903; no eggs laid 1904; 2 pairs failed to breed 1905; birds returned, no breeding 1906, 1907; colony extinct 1909.

Single bird attempted to build 1922.

Attempts at reintroduction unsuccessful 1938, 1939.

3. Grassholm, Pembrokeshire

As with Lundy, we have confined ourselves to information not given by Gurney. Gannets certainly bred here before 1864 (**250**) and almost certainly before 1860 ('few nests') (**133*a***). In 1883 there were 20 nests (**195**). In 1889 a party landed from a gunboat, killed many old birds and destroyed eggs (**62**), but in about that year (**198**) the colony was said to be larger than that on Lundy (which had 70 nests in 1889). On 11 March 1903 (evidence from minute-book), F. M. Ogilvie (**177**) delivered a lecture to the Ashmolean Natural History Society, in which he stated that perhaps 200–250 pairs were breeding (the non-breeders present were estimated to be 20 % of the total numbers). Correspondence with Mr Lewis Balfour (**257**) and examination of the catalogue of the Ogilvie collection (**148**) indicates that Ogilvie definitely visited Grassholm in 1889, though he may have made subsequent visits.

In 1890 over 200 pairs were present (**194**), and in this year Mr J. J. Neale took over the island (**195**) and attempted to stop the persecution which the gannets were suffering at the hands of shooters, fishermen and egg-raiders. Some success was attained at first with this protection. Gurney records in a paper (**93**), but not in his book, that the number of nests increased from about 240 in 1893 to fully 300 in 1895. But plundering went on almost annually (**196**), and there was a great egg raid in 1898 (**194**). In 1903 Gurney (**95**) counted between 324 and 340 adults, at least, on the rock. This should represent between 250 and 300 pairs. In 1905 the number did not exceed 300 pairs (**12**), and as a result of 'trespassers and herring gulls' there had been no increase in the previous few years.

The population never rose above 300 pairs before 1914 (**194**). After 1919 the number of pairs rose considerably; in 1922 (**105**) there were 800–1000 breeding pairs, and about 3000 birds in all; in 1924 (**1, 2**) at least 1800 pairs, probably 2000, were estimated to be present from photographs in which 1930 adults were counted. In 1925 (**130**) numbers of nests were found in which two eggs or young were present. In 1928 (**14**) photographs show the colony to be very thick, and the population 'had been almost doubled' in the last few years (**208, 302**). In 1930 (**15**) fire broke out on Grassholm on 9 June, but was extinguished by the Royal Navy before it reached the gannets' area. In 1933 (**194**) another photographic census gave 4750 nests. In 1934 (**206**) thousands of gannets were breeding at 2 ft. beak-range on 8 July; they practically covered one side of the island. In 1937 (**133, 195**) an estimate gave 5000 nests, and photographs taken in this year, compared with photographs of the same groups in 1928, showed that in nine years the birds had spread on to most of the flat ground above the top of the cliff on the north side of the island (**209**). In 1939 another estimate gave *c.* 6000 occupied nest-sites (**292**), and yet another an increase of 5–10 %, i.e. of 250–500 pairs (**262**). In 1940 the island was purchased by Mr Malcolm Stewart (**303**). There is a good map of Grassholm, showing the gannetry, in **133*a***.

Summary

Possibly breeding 1820.

Probably breeding before 1860, 'few nests'.

Certainly breeding 1864.

20 nests 1883; 250 nests 1886; *c.* 225 pairs 1889.

Over 200 pairs 1890; 240 nests 1893; 300 nests and plundering 1895; great egg raid 1898.

250–300 pairs 1903; under 300 pairs and very few young reared 1905; 100–130 young reared 1906; *c.* 300 young reared 1907.

c. 300 pairs up to 1914; increase 1919 onwards.

800–1000 pairs 1922; 1800–2000 pairs 1924; flat ground north side not occupied 1928.

4750 nests 1933; one side of island practically covered 1934; *c.* 5000 nests and flat ground on north side occupied 1937; 5750–6000 nests 1939.

4. Great Orme's Head, Caernarvonshire

In mid-May 1941, Mr P. J. Dyne(**272**) informs us, some gannets were observed by two boys(**270**, **298**) flying round under the lighthouse on Great Orme's Head, and alighting on a ledge of rock 4–6 ft. wide (covered with some gravelly pebbles) about 30 ft. above the level of the waves, on the cliff 200 yd. south-west of the lighthouse. A few days later one of the boys, a reliable observer who was quite familiar with the gannet, saw only two gannets, but these were in occupation of the ledge, and were seen pairing. Gannets were not seen here later, as far as we know, and were certainly not in evidence when one of the writers paid several visits in August 1941(**276**).

Summary

One pair present but not breeding 1941.

5. Little Skellig, Kerry

The history of this gannet colony up to 1938 has been summarized recently by one of the writers(**73**). This summary omitted the fact that, as late as 1869(**10**), the rock was rented for the taking of gannets' feathers and young, and that the colony was listed in 1870(**36***a*).

In 1939 Miss Clemence Acland(**252**) visited Little Skellig, and, while unable to make a direct count, confirmed the general fitness of Mr S. Marchant's figures for 1938. On 29 July 1941 air photographs were taken(**300**) of the north face of the rock, on which Marchant(**142**) estimated 5000–6000 pairs in 1938. A count of the nests visible in the photographs on approximately half the occupied area of this face gave a figure of about 2800 occupied nests.

Summary

Breeding 1700; an 'incredible number' breeding *c.* 1748.

Breeding 1828; 500 pairs, young eaten 1850; young and feathers taken 1869; breeding 1870.

c. 30 pairs 1880; 150–200 pairs 1882; increasing 1884.

Several thousand pairs 1890; many thousand 1896.

15,000–20,000 pairs 1906, 1908.

8000 pairs 1913; range extended 1914.

10,000 pairs, 'almost every available ledge occupied' 1930.

9000–10,000 pairs 1938 (west 1000; north 5000–6000; south 3000) and about the same number 1939 and 1941.

6. Bull Rock, Cork

To the account, already published(**73**), of the history of this colony up to 1938, we have only one historical item, previously overlooked, to add. O'Connell(**176**) mentions that in 1884, the year in which the lighthouse was built on the Bull, a few gannets were also breeding on the Cow. His account, however, is in the form of a bare and bald statement, and we are unable to place the Cow in the list of past and present breeding places. O'Connell's further statement, that at this time probably more gannets were breeding on Bull Rock than on Little Skellig, seems, from the other evidence already published, to be true.

It is also perhaps worth recording that Newton, who told Gurney(**95**) that in 1899 he saw 'a hundred or so' gannets on the Bull, states elsewhere(**173**) that the number of gannets frequenting the rock in that year appeared to him 'to be very small'.

In 1939 Messrs L. P. Madge(**293**) and H. E. Wall(**307**) visited the rock on 18 August, and estimated the number of birds on the west side to be of the order of 1000, and on the north (where Marchant(**142**) found 24 nests in 1938) in the neighbourhood of 50. One of the lighthouse-keepers who had helped Messrs Carroll and Montgomery (**110**) to climb all over the rock in 1936, told Madge that he estimated 2500 nests in 1939, and 2000 in 1938; it should be remembered that Carroll and Montgomery estimated the population in 1936 at 2000–3000 pairs. These estimates are certainly bad exaggerations, and useless from the point of view of the census—the careful documentation of Marchant's account (442–500 pairs in 1938) puts them in their proper perspective. However, it appears probable, from both Madge's and the lighthouse-keeper's accounts, that there was a considerable increase in 1939 over the previous year's population; the captain of the lighthouse tender, in conversation with Madge, was also of this opinion. It must be remembered that such accounts are much more likely to be accurate when dealing with comparative rather than absolute figures—it is possible to accept an account of an increase without accepting the figures that accompany it.

We have therefore, tentatively, put the 1939 population at 550–600 pairs.

Summary

Birds first seen on rock 1853; first nests found 1856; 11 pairs 1858. 'Many hundreds' but only few eggs 1868. Up to 1000 pairs 1884; lighthouse built

1884–5; possibly 500 pairs 1889. 100–110 pairs 1891; greatly diminished 1896; *c.* 100 pairs 1899. *c.* 1000 pairs 1902; 300 pairs 1908. 250 pairs 1913. 400 pairs and birds increasing 1930. 2000–3000 pairs (error) 1936; *c.* 450 pairs 1937; 442–500 pairs 1938; 550–600 pairs 1939.

7. Great Saltee, Wexford

The following can now be added to the account (**73**) already published.

In 1937 (contrary to the previous account) one young one is known to have been produced. It was believed to have been killed by a herring gull. An adult pair which may have been the parents of the victim was observed earlier in the summer frequenting a different part of the island (**285**).

In 1938, 3 pairs certainly hatched eggs (**269**). One of these was taken by a great blackback (not 'herring gulls' as previously recorded) when the observer put the parent off its nest (**269, 288**). Both the other two were reared (one chick hatched before 7 June (**274***a*))—one of these was previously recorded as 'fate unsettled'.

In 1939, at the end of May, two observers carefully searched the whole island (**264***a*). A party of about 6 gannets was seen fishing off the coast, but there was no sign of a nest.

In mid-May 1943 two pairs of gannets were present (**242***a*). There was one nest with an egg which was taken, probably by a gull.

Summary

2 pairs, 2 eggs, both destroyed 1929. 1 pair, no egg seen 1930. 2 pairs, 2 eggs, no young reared 1932; 1 pair, young reared 1933. 1 pair 1934; 1 pair, nest 1935; 1 pair 1936. 2 pairs, 1 young hatched but not reared 1937. 3 pairs, 3 eggs, 1 egg destroyed, 2 young reared 1938. No pair proved to occupy a site 1939. No information 1940–42. 2 pairs, 1 egg, egg destroyed 1943.

8. Stags of Broadhaven, Mayo

C. Smith (**205**) at the end of his account of Little Skellig, published in 1756, writes: 'I have been informed, that there is another rock on the north coast of *Ireland*, where they alight and breed in the same manner, and no where else in this kingdom.'

A. E. Knox (**223**) states: 'It used, when I was a boy, to breed, but not in numbers, on the Stags of Broadhaven. I cannot say that I have seen their nests, but I have shot the young birds as well as the old ones on the wing, when passing through these islands in an open boat. The young ones were well able to fly, but apparently had only lately left the nest. I speak of many years ago.' Knox was born in Dublin on 28 December 1808, the son of John Knox of Castlerea, Mayo. He went to Oxford as an undergraduate, thence into the Life Guards, from which he retired in 1835, soon afterwards taking up his abode in Sussex (**11**). This biographical detail is quoted to enable us to fix the period of his boyhood, and thus the period at which he observed this station. We put it between 1818 and 1835, most probably between 1823 and 1828.

J. F. Townsend (**223**) sailed past the Stags in July 1836, and saw hundreds of young gannets near the vessel, and 'vast numbers of old and young about the rocks'. He wrote: 'There cannot be the least doubt that the gannet breeds at Broadhaven. In every sense they seemed quite "at home" there.'

A. G. More (**151**) sailed by the Stags on 30 June 1873. He writes: 'We ran down before the wind and round the "Stags" of Broadhaven. Saw no Gannets on the rock.'

In 1882 a keeper at a nearby lighthouse told Ussher (**229**) 'the gannet does not breed on the Stags'. By 1911 Ussher (**230**) was able to write: 'Gannets do not breed on the Stags of Broadhaven, nor anywhere in Ulster or Connaught, their only Irish colonies being on the Little Skellig and the Bull Rock.' Ussher (**231**) had previously written: 'It seems very doubtful whether this bird even bred on the Stags of Broadhaven, which I saw in 1898.'

In 1939 R. F. Ruttledge (**301**) questioned fishermen who stated that the gannet had definitely not bred in the last 15 years, i.e. since *c.* 1924. C. V. Stoney (**304**) visited the Stags of Broadhaven twice between 1928 and 1930 and found no signs of breeding.

In 1939 W. B. Alexander (**253**) was told by one of the lighthouse-keepers at Rathlin O'Birne that in recent years gannets had begun to breed on the Stags. He had not seen this himself, but had been told by members of the Irish Lighthouse Relief Ships which had passed the Stags on the way from Eagle Island to Rathlin O'Birne. These stated that about a dozen pairs were now breeding. Accordingly we got in touch with Miss Clemence Acland (**252**), Major R. F. Ruttledge (**301**) and Mr Angus Gore-Booth (**260**). Miss Acland was, unfortunately, prevented from going out to the Stags by bad weather, but the other two observers visited the rocks independently on 26 July. Major Ruttledge saw over 12 gannets between Porturlin and the Stags, but none was nesting, and a 60-year-old fisherman told him they never had. Mr Gore-Booth saw 10 fishing, but none nesting, though he landed on the third Stag from the shore, went round and surveyed all the faces, and saw none on the rocks. Again, the fishermen told him that they had not seen any nesting.

Summary

Possibly breeding *c.* 1756, *c.* 1823–8, 1836.

Not breeding 1873, 1882, 1898, 1911, 1924, 1928–30, 1939.

(*d*) EAST BRITAIN GROUP

9. Bempton Cliffs, Yorkshire

In 1924 it was noticed that a pair of gannets frequented the Black Shelf all the season, driving the

other birds away(**239**). In 1925(**34**) a nest was actually built on 11 July, but no egg was laid. In 1926(**240**) the birds made a further attempt, but kittiwakes carried off the nest material and finally drove the gannets away. No report is available for 1927, but in 1928(**241**) the birds again tried, and suffered the same fate at the hands of the kittiwakes. In 1929(**242**) they made two attempts at a nest, but once more the kittiwakes made them desert. No reports are available for 1930–6, but in 1937(**145**) a pair was present and laid an egg, which was taken on 11 June(**261**). In 1938(**136, 146, 261, 264, 278**) two pairs were present, an egg was in the nest on 12 June, a young bird was seen on 12 July, and in early August it was photographed and ringed. In 1939, at Whitsuntide, four pairs were seen(**303**), from a boat, three-quarters of the way up the cliff known as Black Cliff End, each in occupation of a nest-site. Of these, one pair is known(**48, 264**) definitely to have produced young.

In 1940(**147**) birds were on the cliff and probably nested; but no one went down, and it was not possible to see young birds from the cliff-top. Nothing definite was recorded about breeding in 1941(**147***a*), but birds were reported to have been about the cliffs again. For 1942 the report is: 'Has nested again at Bempton, but no details are available'(**3***a*).

Summary

One pair present 1924–6, 1928–9.

One pair present, 1 egg taken 1937; 2 pairs present, 1 young reared 1938; 4 pairs present, 1 young reared 1939.

Birds present, but breeding not proved 1940, 1941; probably breeding 1942.

10. Bass Rock, East Lothian

Gurney(**95**) is at his most comprehensive on the subject of the Bass Rock, and those who read his excellent monograph in conjunction with these notes and summaries will understand the scope and thoroughness of his researches. The information that follows is purely that not given by Gurney.

In about 1597(**153**) the 'farming' of gannets on the Bass Rock was becoming a very profitable concern. In 1710 Sir Robert Sibbald(**201**) records the whole surface of the rock as covered with gannets; that they also nested occasionally on the neighbouring islands of Craigleith, Lamb, Fidra (and Ibris?), and that at the beginning of August young were sold in Edinburgh for 2*s*. or more, feathers being used for palliasses. Mackay(**160**), whose book was not seen by Gurney, gives an account (1723) of the Bass gannets and the use of their feathers for beds, and flesh for food. Sinclair(**203**) in 1793 just mentions the colony, as does the anonymous author of the *Traveller's Guide*(**9**) of 1798.

By the beginning of the nineteenth century(**188**) 10 gal. of oil were drawn from the gannets' fat annually by the inhabitants. The price of oil was about 2*s*. 6*d*. a gallon (and one gannet, according to Gurney, yielded ⅞ lb. of oil; 10 gal. was thus equivalent to about 100 gannets).

In 1806 a guide-book mentions the gannets(**210**).

MacGillivray(**22**) paid his first visit to the Bass Rock on 13 May 1831 and found 'every part of the mural faces of the rock, especially towards their summits, was more or less covered by them'. He found 300 nests on the gravel slope near the landing-place. 'The number [of gannets]', he writes, 'might be estimated at twenty thousand.' In 1834 MacGillivray found 14 nests with 2 eggs. In 1835 he took Audubon to see the colony. At this time he records that at least 1000, at most 2000 and generally 1500–1600 young were killed yearly. Prices were: plucked young, 6*d*. to 1*s*.; young for stuffing, 2*s*.; adults, 5*s*.; eggs, 1*s*.

In 1839(**85**) the Bass was let for £30, on a 19-year lease, to a tenant in Canty Bay. Gurney states that from about 1856 the tenant of the Bass was Mr Geo. Adams, but 'what rent he paid I have no means of knowing'. One authority(**167**) gives this as £50–60 p.a., and another(**125**) at £60–70 p.a. Certainly between 1856 and 1869 young were sold in Edinburgh and other neighbouring towns at 8*d*. or 9*d*. each, 1*s*. 6*d*. each (1860), and 1*s*. 8*d*. each. Customers (who included many Irish labourers) baked the young gannets after wrapping them in rhubarb leaves. It was stated that at this time 1200–2000 were taken in a year(**38, 125, 167, 186**). In 1869 the breeding population was estimated at 12,000 birds, but the authority for this (M'Donald in **183**) gives 300,000 for Sula Sgeir, and thus cannot be regarded as reliable. In 1871 an estimate(**87**) gave 20,000 birds, and this was quoted again(**141**) for the 1872 population; this figure can scarcely be worth a moment's consideration. In 1873(**216**) young were taken for oil, but the numbers appeared to be increasing. In the nineties O. A. J. Lee(**126**) took what must have been among the first photographs of wild gannets.

Though Gurney makes much of Evans's(**69**) estimates of the numbers of gannets on the Bass in 1901 and 1904, he does not quote Evans's estimation of the number of nests in 1904 as 'fully 3000' but quotes only his estimate of the numbers of adults as 7000–8000. He uses a lot of complicated argument based on Evans's photographs (involving hazards as to the number at sea) to make the figure equivalent to *c*. 3150 pairs—we are using Evans's figure.

It is worth mentioning that in the first fortnight of August 1904 Gurney(**94**) ringed 40 young and 50 adult gannets—the first time that this species had been marked; and that a Bass Rock nestling ringed on 30 July 1913 was recovered in Norway on 28 January 1917(**248**).

In 1929 a careful count by J. Bain, Principal Lighthouse-keeper(**188**), gave 4147 nests. In September 1934(**50**) most young had taken their first

flight, but there were many at all stages of development. This was ascribed to the robbing of first eggs, partly by herring gulls. An estimate in 1936(**191**) gave 4150 nests, and in 1939 Mr J. Bain's count gave 4374 nests on 9 July(**256**). The herring gulls on the Bass Rock have increased from *c.* 5 pairs in 1934 to *c.* 200 in 1939. 100 pairs of gannets lost their eggs through these gulls when photographers forced them to desert their nests. Mr Bain writes: 'As long as there are herring gulls on the Rock I don't suppose there will be any perceptible increase of gannets as all the available cliff sites are occupied and when attempts are made to occupy the slope above the eggs are usually taken within a day or two.'

Summaries

General. Gannets known in North Sea *c.* sixth century (Beowulf).

Mentioned dates fifteenth century (*Scotichronicon* (1447), Papal Commission).

Mentioned 15 dates sixteenth century (Household books James IV (3 times), Major, Boece, Swave, Turner, de Beaugué, Magnus, Gesner, Caius, Leslie, Scots Parliament Act, Aldrovandi, Moniepennie).

Mentioned 22 dates seventeenth century (Camden, Taylor, Jonston, Household books Lord W. Howard (twice), Brereton, Blaeu, Harvey, Tradescant Museum, Childrey, Ray, Willughby, Merrett, Household books Duke of Lauderdale (5 times), Household books Sir John Lauder, Sibbald, Dalrymple, Drummond).

Mentioned 13 dates eighteenth century (Morer, Dalrymple Charter, Sibbald, Mackay, Defoe, Household books Sir Hugh Dalrymple (4 times), Watson, Pennant, Sinclair, *Traveller's Guide*).

Mentioned 33 dates nineteenth century (Stark, Bullock and Strickland, Jardine (twice), Fleischer, Selby, Wolley (3 times), Glasgow botanists, le Bas, Harvie-Brown, Napier, 'Punt-gun', M'Donald, Gray, Preyer and Zirkel, Gröndal, Lumsden, Stuart, British Association, Cunningham, Booth, Witherby (twice), Adams, Earl Grey, Gurney, MacGillivray, Audubon, Fleming, Lee, Graham).

Breeding population. 'Marvellous multitude' 1521; 'incredible number' 1526; 'could not be easily estimated' 1535; 'plenty' 1555; 'numbers obscure the sun' 1570; 'more abundant than Ailsa Craig' 1578.

'Abundance, breeding on the sides of the rocks' 1635; grass top entirely covered 1641; 'multitudes', 'innumerable' 1661; surface almost covered 1693.

Whole surface covered (also breeding Craigleith, Lamb, Fidra?) 1710; still multitudes, nesting on the sloping part 1769.

Still nesting on the summit 1816.

300 nests on gravel slope near landing, estimate *c.* 10,000 pairs 1831.

Estimate 5000 pairs 1847 or 1848.

Estimate (based on doubling number of young taken) *c.* 3400 pairs 1850; had not yet abandoned upper slopes 1859.

Still some nesting on the grassy slopes 1862; nesting well above 1904 limits, estimate *c.* 6000 pairs 1869.

Estimates (of little value) *c.* 10,000 pairs 1871 and 1872; increasing 1873.

Less molestation 1885.

Decrease to 3000 pairs 1904; further protection 1905; increase 1909.

Estimate *c.* 3250 pairs 1913.

Count 4147 pairs 1929.

Estimate 4150 pairs 1936; count 4374 pairs 1939, slope above cliffs not occupied.

Use of the birds by man. There are definite records of gannets being taken for food (numbers of young taken in brackets) in the years 1511, 1521, 1525, 1529, 1592, 1597, 1618, 1623, 1624, 1633, 1635, 1638, 1661, 1671, 1674 (118), 1675 (1060), 1676 (1150), 1677 (985), 1678, 1689, 1710, 1723, 1764–7 (1296 p.a.), 1768, 1821, 1831–5 (max. 2000, min. 1000, mean 1500–1600), 1839, 1841, 1848 (1800), 1850 (1700), 1856 (eggs sold), 1860, 1865 (*c.* 1500), 1874 (800), 1876 (800), since when no record of young taken; but 1880 (1800 eggs taken), 1885 (2000 eggs taken), since when no record of large numbers of eggs taken (Wild Birds Protection Act 1880).

Production of oil and grease is recorded in 1493, 1526, 1544, 1570, 1764–7, *c.* 1800–25 (10 gal. p.a. = 100 young), 1873, 1875, when it seems to have ended.

The use of feathers is mentioned in 1535, 1570, 1638, 1710, 1723 and 1764–7, but not afterwards.

The use for human food of fish regurgitated by gannets is recorded in 1521, 1535, 1548, 1555, 1578 and 1610; this practice seems to have been discontinued over 300 years ago.

11. Isle of May, Fife

Before 1850 the gannet used to breed here according to Jardine(**249**), who writes: 'We have shot it there and taken the young from the nest.' In 1922 (**26**) a pair of gannets attempted to nest here, but without success.

Summary

Breeding before 1850.

Unsuccessful attempt at breeding 1922.

(*e*) WEST BRITAIN GROUP

12. Calf of Man, Isle of Man

Gurney(**95**) and, following him, Williamson(**245**) quote the vague mention of gannets in Buchanan's *Rerum Scoticorum Historia* (1583): 'Frequens est cuniculis, avibusque marinis, eoque maxime genere anserum, quas Solanas vocamus'—as applicable to the Isle of Man. If indeed he personally saw the

original Latin reference, he must have misquoted it; the phrase refers directly to Ailsa Craig.

On the other hand, evidence collected by K. Williamson (**245**) is very strongly suggestive of the existence of a gannetry on the Calf of Man in historical times. Camden's *Britannia* (1586) reads: 'Calfe of Man...exceeding great store...of those ducks and drakes which (breeding of rotten wood as they say) the Englishmen call them *Bernacles*, the Scots *Clakes*, and *Soland Geese*.' In 1648 William Blundell found on the Calf 'sea fowles geese, which ...are called barnacles, but by the Scots claik geese and soland geese, etc.' Blundell was probably copied by Heyleyn (1675), Denton (1681), Gibson's edition of Camden (1695), Cox (1700), Rolt (1773) and the *Chronicon Manniae* (1784). Of these writers most were muddled by the confusion with the barnacle goose, though Gibson's edition of Camden seeks to correct this confusion.

In 1652 James Chaloner (later Governor of the Isle of Man) commissioned Daniel King to engrave plates of the birds of the Calf of Man for his *Short Treatise of the Isle of Man* (1653). In these plates a fine picture of a great auk appears, as does an equally fine one of a pair of gannets standing on a ledge.

During the summer of 1939 a pair of gannets (adult birds) was often seen on the south-west cliffs of the Calf of Man, near the Burrow and Stack (**246**).

Summary

Possibly breeding 1586, 1648, 1652.

1 pair present, not breeding, season 1939.

13. Scar Rocks, Luce Bay, Wigtownshire

On 25 May 1883 R. Service, according to Gurney (**95**), found 2 gannets' nests on the Big Scaur, one of them containing a broken egg; he saw the pair of old birds flying close at hand. Gurney suggested that this might have been an offshoot of the Ailsa Craig colony.

On 6 June 1939 (**118**) some were seen on the wing here, and 6 were sitting; no egg was found, but gannets sometimes do not lay until 10 June. On 5 July, 3 or 4 birds were seen resting on the rock, and on a further visit on 1 August the same observers (**165**) found a single nest in which was a young gannet. No visit was possible by sea in 1940 (**296**), and aerial observation (**300**) disclosed no trace of gannets. In 1941, however, a Coastal Command aircraft flew over the rock and an observer (**299**) noted more than 20 gannets flying about. On 17 May of the same year a visitor by sea (**293** *a*) had seen none. In 1942 observations from the air showed the presence of nesting birds, and on 14 July J. M. McWilliam (**296**), who had first proved breeding in 1939, landed and found about 25 nests, many containing young (**166**). In early June there may have been about 40 nests, but a party took some eggs. On 24 June 1943 Mr McWilliam again landed and, with a companion, found about 45 pairs of gannets nesting; young were just beginning to hatch out.

Ornithologists and fishermen have visited the Scar Rocks on several occasions since 1918, but have never mentioned gannets breeding there, until 1939.

Summary

2 nests 1883.

2–6 pairs, 1 nest, 1 young reared 1939.

Breeding not proved 1940; breeding not proved but possibly 10 pairs 1941; *c.* 25 pairs breeding 1942; *c.* 45 pairs 1943.

14. Ailsa Craig, Ayrshire

Up to 1907, this account is simply confined to corrections and additions to that of Gurney (**95**).

Buchanan's note of 1583 (see p. 181) quoted by Gurney as referring to the Isle of Man, concerns this colony. In *c.* 1791 gannets and other birds 'filled the air' (**8**). In 1791 (**202**) and 1792 (**103**) the tenant paid the Earl of Cassilis £25 p.a. from the profits on gannet feathers and rabbit skins. In the nineteenth century the Craig was often discussed but, as regards the gannets, by no means critically. In 1813 there were 'immense flocks' of gannets (**56**), and the feathers were sold commercially. In 1824 (**157**) the Craig rent was £30 p.a. In September 1843, 100 gannets were shot (**223**) by a 'gent' who had the shooting over Ballantrae. To the references given by Gurney we must also add accounts given by Hill, 1837 (**106**); Donaldson, 1854 (**61**); Gray, 1864, 1871 (**86**, **87**, **88**, **89**), who hints that there was no more room on the ledges; Buckland, 1871 (**44**), who states that young were probably still being taken; McConnell, 1894 (**156**); Kearton, 1897 (**120**); Rose, 1898 (**192**) and Paterson, 1901 (**181**).

Estimates of 5000–10,000 pairs in 1868 (**124**) and of 6000 pairs in 1869 (M'Donald in **183**) cannot be too closely relied upon; the next computation of the population was Gurney's—probably after his visit in 1905. He put the total number of *individuals* at *c.* 6500. His estimate, and that of Salmon (**65**)—7500 *pairs* in 1935—are fully discussed in a previous paper (**236**). In general we can take it that Gurney's estimate was probably too low, and Salmon's possibly too high.

In 1907 the proposed quarrying operations near the Main Craigs were causing some concern to the British Ornithologists' Club (**193**) who were, however, assured by the Marquis of Ailsa (**3**) that there was no danger to the gannets.

In 1913 (**121**) there may have been a slight increase in the number of gannets, in spite of the fact that heavy practice gunfire in the Clyde is thought to have driven away nearly all the other sea birds. It is not certain, however, that this was not due to changes in the distribution of food. In 1914 (**168**) large numbers of gannets occupied the top ledges.

Unpublished observations by D. Macdonald (**294**) which he has kindly made available to us, refer to

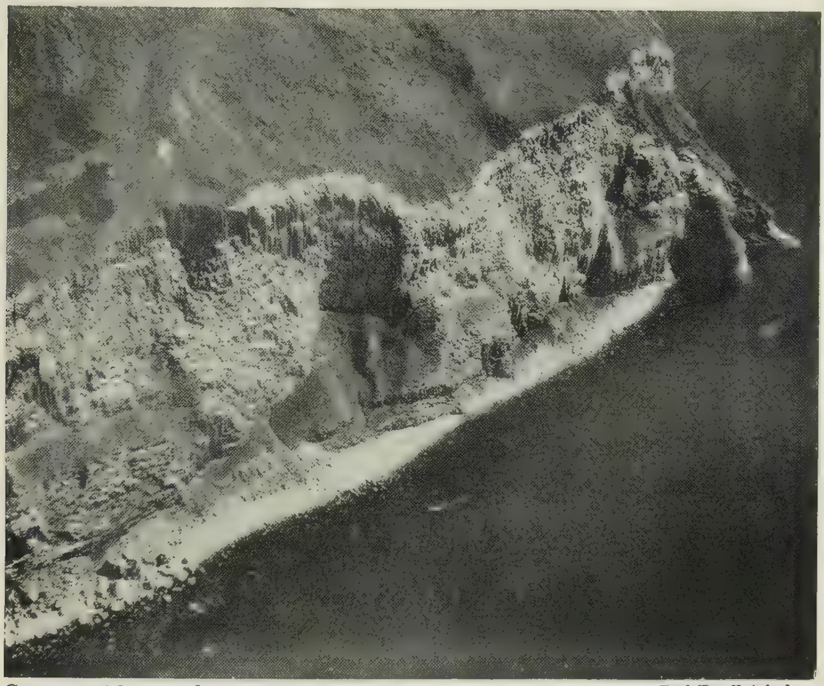

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Photo. 4. Close view of the gannet cliffs of Ailsa Craig, approximately from the west, 24 August 1941. Most of the total population of 3518 breeding pairs in that year bred on this part of the cliffs, from the Mare on the left, to Stranny Point on the right. *c.* 400 ft. to top of these cliffs. Reproduced by permission of Coastal Command, Royal Air Force.

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Photo. 5. Gannets fighting on the boulders beneath the Barestack, Ailsa Craig, early April 1939. Fights over nest-sites or nest-material often take place at this season. They may begin on a ledge—from which the birds may flutter and fall, with their bills interlocked, 400 ft. to the beaches or sea below—and continue for 2 min. or more.

Table 1. *Analysis of the Ailsa Craig colony in recent years; all figures stand for the number of pairs*

	1922	1923	1924	1925	1929	1935	1936	1937*	1938*	1939	1940	1941	1942
Barestack			F.O.	—	—	—	92·5	147	96	93	131	33	71
Northwards of Ashydoo	450† (Northwards of Ashydoo to A2)			V.N.I. (Northwards of Ashydoo to A2)	—	—	272·75	370	290	328	295·33	141	250
Ashydoo, A1		—	—		—	—	211·5	188	189·5	256·5	254	79·25	251·5
,, A2					—	—	47	34	32·75	69	76	20	48
Balvaar	500†	—	—	—	—	—	228	649·5	530·5	453·5	470·5	292·5	417·5
Balvaar-Cairn	—	—	—	—	—	—	63·5	68	59·33	65	68	38·3	60
Cairn	—	S.I.	—	—	—	—	603	813·7‡	606	511	694	594	796·5
Barrheads, S.	—	—	—	—	—	—	19	43	38	35	§	15	48
,, Mid	—	—	—	—	—	—	9	14	19	36	23	44	214·5
,, N.	—	—	—	—	—	—	132	91·5	95	46	149	42	40
Cairn-Mare	—	—	—	—	—	—	379	290‡	452	513·5	518·5	298	396·2
Mare	—	—	—	—	—	—	1583·5	1936‡	1688	1954	2127	1181	1093
Mare to Stranny Point, S1	—	—	—	—	—	—	101·5	86	81·33	91	100	52·5	91·7
,, S2	—	—	—	—	—	—	67·5	61·7	60·4	49	74	15	46
,, S3	—	—	—	—	—	—	114·75	175·2	115·33	125	156	82	162·5
,, S4	—	—	—	—	—	—	215·5	269	185·5	173·5	258·5	158·5	233·7
Main Craigs, Top	—	—	—	—	—	—	94	266·5	272	192	263·33	158·5	225
,, Main	250†	—	—	—	—	—	429·5	346·5	401·25	290	373·5	160·8	267
,, E.	—	—	—	—	—	—	103·5	75	104·5	82	122·5	75·3	61·4
,, E. Top									24·5	17	24	11	12
,, Far E.							33·67	20	45·8	39	54·25	25·9	43
General	—	—	P.Y.O.I.	—	—	—	—	—	—	—	—	—	—
Total by count	—	—	—	—	—	—	4800	2905	5387	5419	6232	3518	4829
Total by estimation	—	—	8000	—	7000	7000	—	3040‡		—	—	—	—
Accepted grand total	c. 4900‖	—	c. 8000	—	c. 7000	c. 7000	4800	c. 5945	5387	5419	6232	3518	4829

Symbols: * For notes on the 'oiling' of gannets in these two years see (**234**). F.O. first occupied; † estimation; V.N.I. very noticeable increase. S.I. slight increase; ‡ estimate by alighting method; § with Stranny groups; P.Y.O.I. reported 'peak year of increase'; ‖ writers' calculation based on Macdonald's estimates. Nearly all figures are the mean of several counts by different observers; totals to nearest pair.

Summary

Breeding first recorded, 'plente' 1526; abundant 1549; abounds, but not so abundant as at Bass 1578; abundant 1583; many 1587.

Abundance, eaten by man 1635; great plenty, eaten by man 1696.

Mentioned at second-hand 1710, 1718, 1722; rent £33 p.a. 1772.

Gannets, etc., 'filled the air' *c.* 1791; annual rent Craig (gannet feathers and rabbit skin trade) £25 1791 and 1792.

Immense flocks 1813; feathers sold commercially.

Rent £30 p.a. 1824; rent still derived chiefly from sale of feathers 1837.

Maximum of 500 young taken a year certainly 1853–*c.* 1860, possibly up to *c.* 1880, eggs taken later.

Estimates *c.* 7500 pairs 1868, *c.* 6000 pairs 1869.

Suggestion that ledges were full up, young taken 1871.

'Thousands' 1901; possibly *c.* 3250 pairs 1905; quarrying round 1906.

Increase 1913; large numbers top ledges 1914.

c. 4900 pairs 1922; increases recorded 1923–5; Barestack first occupied and estimate *c.* 8000 pairs 1924; *c.* 7000 pairs 1929 and eggs probably taken until this date.

c. 7000 pairs 1935; 4800 1936 and Main Craigs, Far East first found occupied; *c.* 5945 1937; 5387 1938 and Main Craigs, East Top first occupied; 5419 1939; 6232 1940; 3518 1941; 4829 1942.

15. Islay, South Inner Hebrides, Argyll

In 1703 Martin (**144**) writes: 'The Solan Geese and Culterneb are most numerous here', but G. G. Smith (**207**), in a very complete historical account of the island (1895), makes no mention of the bird whatever.

Summary

Doubtfully breeding 1703; no modern evidence of breeding.

16. Eigg, North Inner Hebrides, Inverness

Monro (**154**) states: 'EGGA...many solan geise.' He visited the Western Isles in 1549. Moniepennie's account (**153**)—'In Egga are Solayne Geese'—was almost certainly copied from Monro, and published first in 1597. We have no evidence of later suspicions that gannets bred on Eigg; no mention is made of such a thing by Evans (**68**) in 1885, or by the MacPhersons (**163**) in 1888.

Summary

Possibly breeding 1549; no modern evidence of breeding.

17. Rum, North Inner Hebrides, Inverness

Monro writes: 'Maney solan geise are in this ile.' Moniepennie expands this: 'the sea fowles lay their egges heere and there in the ground. In the middest of spring time, when the egges are laid, any man may take of them. In the high rockes, the solayne geese are taken in abundance.'

Summary

Possibly breeding 1549, 1597; no modern evidence of breeding.

(*f*) NORTH BRITAIN—FAEROES GROUP

18. Oigh-sgeir Eagach (Haskeir), Outer Hebrides, Inverness

R. B. Freeman (**81**) writes: 'A mile to the south-west of Oigh-sgeir (Haskeir) are five small stacks called together Oigh-sgeir Eagach. They are very inaccessible and the older men of the west side villages maintain that there was once a gannet colony there. The man who told me this would not be more definite than "a long time ago". There are certainly none there now.' Freeman's visit was on 10 July 1939.

One of the writers flew low over Oigh-sgeir Eagach on 30 July 1942 (**276**). Gannets were entirely absent.

Summary

Possibly breeding nineteenth century; not breeding 1939, 1942.

19. Boreray, Stac Lee and Stac an Armin, St Kilda, Inverness

To treat the great central gannet colony at St Kilda it has been found best to follow Gurney until the end of the eighteenth century and, from then on, to set out the information anew, shortly. Until the end of the eighteenth century we have, then, only the following to add to Gurney's account (**95**):

In 1710 Sibbald (**201**) suggested that from St Kilda gannets might colonize the Bass Rock (?). MacAulay's account (**155**)—he was on St Kilda in June 1758—mentions that eggs were taken on Boreray and Stac an Armin, but never on Stac Lee, though young were taken on all three.

Wilson (**247**) says that the minister on St Kilda told him that 15,000 gannets had been captured in a few weeks on Stac Lee before 1827, 'without the least diminution in their amount'. On the other hand, MacKenzie (**161**), who was resident minister from 1829 to 1843—the minister in question—and whose account is easily the best of the early nineteenth century, states that up to 1829 never more than 5000 young were taken (though, in his opinion, the inhabitants could have killed 5000 young and 4000 adults), and that from 1829 to 1843 never more than 2000 young were taken. It is a great blessing that his posthumous notes were published.

In the spring of 1831 Atkinson (**21**) said that the gannets were entirely confined to Boreray—but he *must* have meant the adjacent stacks also; certainly these were occupied in July 1840 (**159**) when some

non-breeders were present. In 1840 MacKenzie records that *c.* 1600 young were taken. In April 1841 MacKenzie told Wilson (**247**) that every family (*c.* 28) got 40–50 gannets a year, i.e. *c.* 1120–1400 in all. Little attention should be paid to the fact that this was in April, since the dead birds, young and adults together, were stored in cletts and used throughout the year. Little attention, too, should be paid to Wilson's figure of 15,000 gannets captured, already quoted. MacKenzie was the minister to whom Wilson spoke, and Wilson must have added 10,000 to the maximum figure that MacKenzie's MS. notes record. This slip, exaggeration or inaccuracy—whichever it is—is a great nuisance; as the figure of 15,000, like Martin's (**143**) exaggeration (in his otherwise estimable work) of 22,600 eaten in 1696, has crept into many accounts as a 'good' record (e.g. see **135**). Wilson's accuracy as an observer can be gauged from the fact that he believed 200,000 gannets to be a moderate computation of the total population.

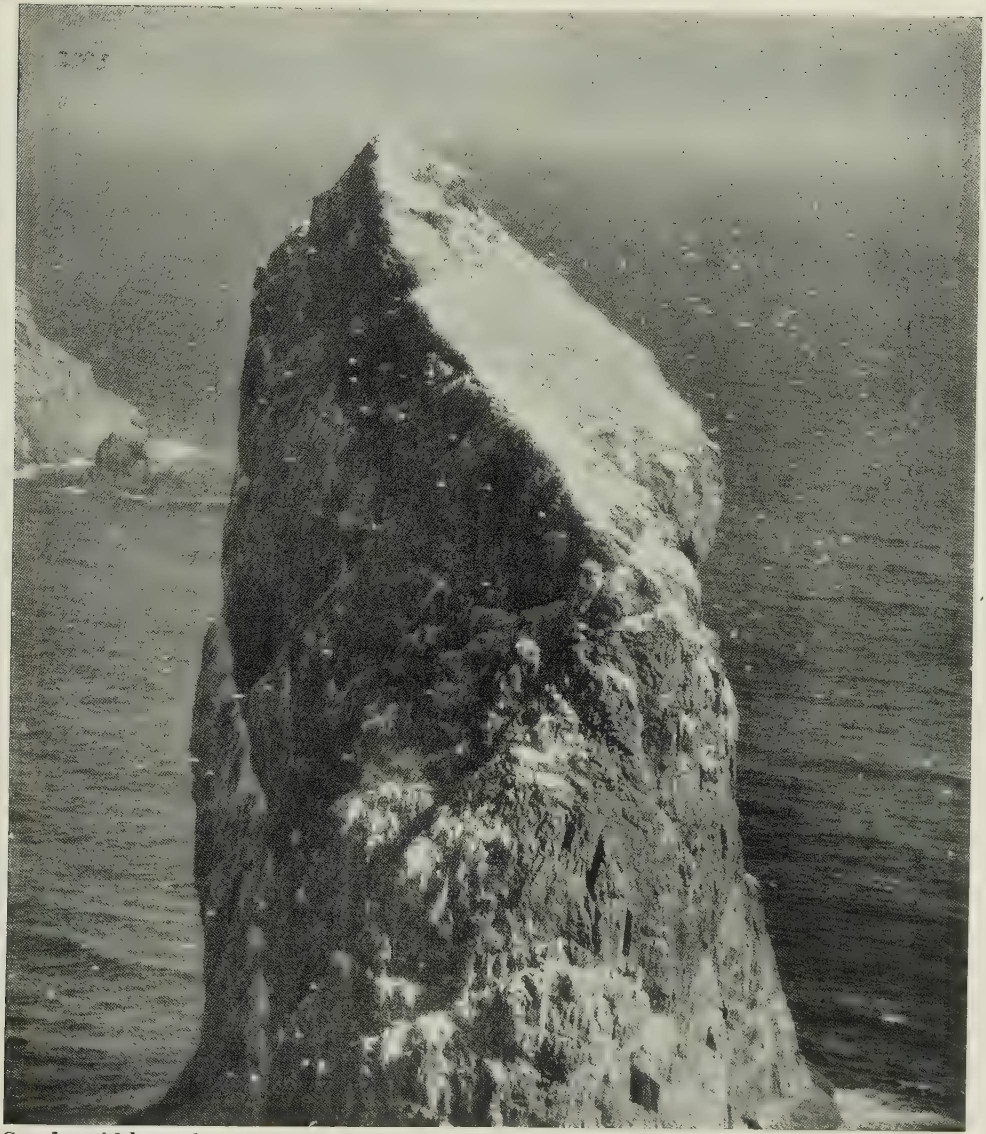
In June 1847 1100 gannets were said to be taken in a single night (**150**). From a visit in 1868 (**66**) we have no useful information save that the inhabitants liked fulmars and gannets best to eat. In about 1869 a sea captain estimated the population at *c.* 50,000 birds (**183**). Sands (**197**), who was on St Kilda in 1875 and 1876, records a great fulmar-fowling industry, though for an account of gannet catching he had to go to Donald Og, an old and crippled cragsman. (Fulmar killing on St Kilda went on steadily, and without diminution, until at least 1921 (**79**). Up to then seldom less than *c.* 9000 young fulmars were taken in a year, and since 1874 seldom more than *c.* 10,000. This industry compares in an interesting way with the gannet killing, which was never on such a large or business-like scale.) There was probably a little gannet killing still on Boreray and Stac an Armin, though Sands does not mention Stac Lee. In 1879 (**40**) Stac an Armin and Stac Lee were 'covered along their whole slopes and summits, and far down their sides, with countless and closely terraced rows of Gannets'.

After a visit from 3 to 17 June 1884 Dixon (**60**) stated that gannets bred in tens of thousands on Boreray and the adjacent stacks, and that Stac Lee was the greatest station. In April 1885 (**52**) three men took 160 adults, and nine men took 500 adults on Boreray in one night. This was considered a great success. In 1887 it was considered that 'the Ailsa Craig or Bass Rock population could be taken without the colony being sensibly diminished (**173**), and Newton was prepared to believe that there might be more gannets on St Kilda than in all the rest of the world beside. (At that time, when the world population was nearly at its lowest, the St Kilda numbers were probably about a third of those in the rest of the world.)

By 1895 (**95**, **164**) the inhabitants were dividing the gannets yearly into 16 shares; each in this year was of 80 young and 120 adults (1280 + 1920 = 3200 in all). In 1902, however (**95**), only 300 were taken, this being ascribed to the drop in the export value of bird oil (though certainly fulmars continued to be taken in the usual large numbers). In 1902 Wiglesworth made his visit (**244**), climbing Boreray and the Stacks on 10 June. He gave a most admirable account of the numbers of gannets. On 14 May the top of Stac Lee had been cleared of eggs by the natives (being prized as food, but to a smaller extent than previously). It might be noted that on 10 June 1902 Wiglesworth found 4 nests on the top of Stac Lee with two eggs in each. Some nests were, at that date, still unoccupied, and he put the total on the top table at *c.* 1500. The men told him that there were more nests on the whole of the rest of the stack than on the summit. Hence he put the total number at 3500–4000. On Stac an Armin there were large numbers, though appreciably fewer than on Stac Lee; put at 3000. On Boreray the natives told him that there were more nests than on the two stacks together; put, therefore, at *c.* 8000; total breeding population 14,500–15,000 pairs—allowing for non-breeders, 30,000 birds. Wiglesworth also notes that the great raid used to be in September, but hints that it had fallen into abeyance. (Harrisson (**100**) points out that information from St Kilda natives was likely to be unsound in Wiglesworth's time. We would agree that the natives' estimation of actual numbers was then, as it was in 1939 (when one was quite definite that the population was three million), unlikely to be accurate. On the other hand (see p. 178), we see no reason to suggest that their estimates of *relative* numbers as between the stacks would be equally inaccurate.)

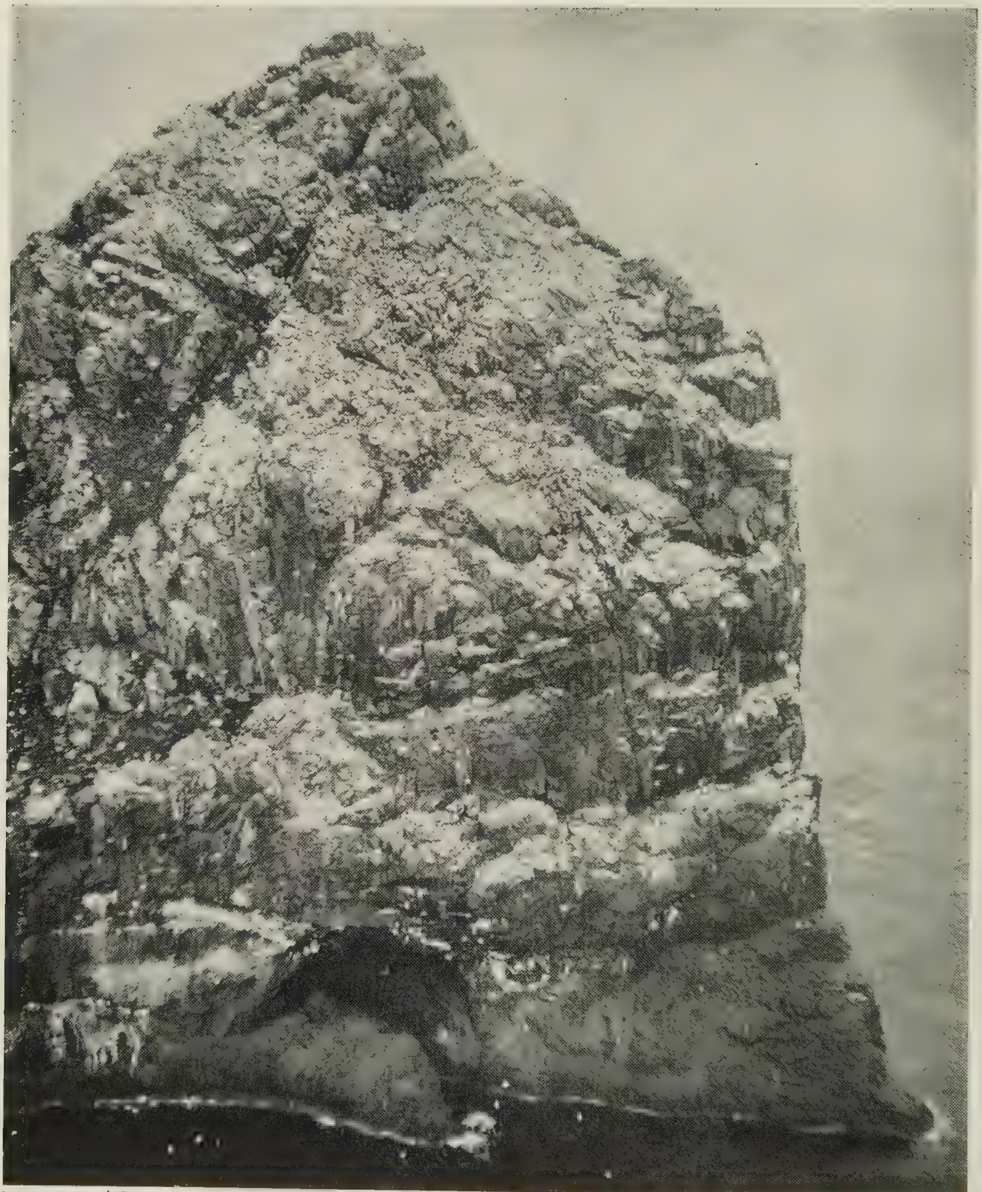
In the spring of 1910 600 adults were caught for food (**49**). By this time young were no longer caught. We have no useful information from the Duchess of Bedford's visit in 1914 (**27**).

In 1931 T. H. Harrisson (**100**, **101**) 'estimated from a boat the numbers on Boreray at 4300 birds, on Stac Lee at 10,000 birds, and on Stac an Arnim (*sic*) at 7000 birds, making a total of 21,000 adults'. He states: 'How many of these were breeding and how many non-breeding, and how many adults were away feeding, it is impossible to say. Also, owing to the difficult conditions under which the count was made, these figures clearly have an extremely wide margin of error.' Wynne-Edwards *et al.* (**65**) suggest that the 'unoccupied birds' were less than 20 % of the total, and that the breeding population was therefore not less than 16,500 pairs. Presumably by 'unoccupied birds' they meant those present on the rock with their mates, or as non-breeders; if so, this is a good approximation, judging from our own observations on Noss, Shetland, at about the same time of year (late July). If we deduct 20 % from Harrisson's figures to give us the number of breeding pairs, we get: Stac an Armin, 5600; Boreray, 3440; and Stac Lee, 8000 pairs; total 17,040 pairs, generalized by Wynne-Edwards *et al.* as 16,500 pairs.



 R.A.F. official photo

Photo. 8. Stac Lee, St Kilda, 30 April 1942, approximately from west-north-west. Height 544 ft. About 2500 pairs were estimated, from other photographs taken by the same aircraft, to be nesting on the sloping plateau at the top. In 1939 the number of breeding pairs on this plateau were about 2000, and on the whole stack about 5000. Reproduced by permission of Coastal Command, Royal Air Force.



R.A.F. official photo

Photo. 9. Stac an Armin, St Kilda, 31 August 1941, approximately from the east. Height 627 ft. From grid counts on this photograph *c.* 2700 pairs were estimated to be nesting on this face in 1941, an increase over the number in 1939, when about 2500 pairs were breeding on the whole stack. Reproduced by permission of Coastal Command, Royal Air Force.

We cannot discuss Harrisson's figures, however, without some puzzlement. Though we know (see Ailsa Craig) that the numbers at a colony may fluctuate considerably from part to part, the difference in the distribution of numbers between the stacks in 1931, as against their distribution in 1902 and 1939, seems to be almost staggering. If Harrisson's figures are anywhere near correct, we must accept an approximate halving of the Stac an Armin and Stac Lee numbers in 1939 as compared with 1931, and an approximate doubling of the Boreray figures. Harrisson is known to have landed on, and climbed, Boreray, but less light can be thrown on his activities round the stacks, and on the westward side of Boreray—he does not state the vantage-point, or points, from which he estimated the number of birds at these places. His count (**100**) on Clagan na Ruskochan must have been made from the top of the cliff of Boreray. We feel that he must have missed the large groups at the north end, Mullach an Eilein, Geargo and Udraclete, which can only be counted from the sea at that end.

Rock	Group
Stac an Armin	N.E. and S.E. faces
Boreray	Geargo
Boreray, W. side	Clagan na Ruskochan
Stac Lee	S.E. face

On 31 May 1939 a party including J. S. Huxley (**287**), E. M. Nicholson (**297**) and J. Fisher (**276**) landed on, and climbed to the top of Boreray from Mr David Robertson's *Escape* and also sailed round the stacks. On 2 June the stacks were again visited by sea in calmer weather. As has already been explained (**174**), and as is clear from Table 2, three-quarters of the population was counted (a third of the whole slowly and accurately with glasses) and the remainder estimated. The number of occupied nest-sites certainly lay between 15,785 and 19,115, and was highly probably in the neighbourhood of 16,900.

On 31 August 1941 a flying boat of Coastal Command, Royal Air Force (**300**), flew round Boreray and the Stacks, taking many photographs, enlargements of which have very kindly been presented to the British Trust for Ornithology. On some of these photographs, with the aid of a grid and, in one case, a hand lens, adult and young gannets at their nests can be finely distinguished and counted. A sample count on the very clearest parts of the photographs indicated that at 20 % of the nests both adults were present. The young were still in the whitish downy stage, or just coming out of it, and appeared as white objects, less clear-cut than their parents. The young and adults were umped together in the counts. Supposing the number of nests containing young to be the same as the number of pairs of adults still present in occupation of nest-sites, and allowing for the 20 % of nests at which both parents were present, the number of adult pairs present is four-ninths of the number of adults and young counted. We thus have the following results:

Map ref.	No. counted	Approximate no. of pairs
2 and 3	6022	2676
5	2164	962
Most of 9	1346	598
13	4612	2050

These figures indicate an increase on the 1939 population, but we have not calculated a figure for the whole population, based on these sample groups, since the situation in a group does not necessarily reflect the situation in the whole and it is possible that the count was inflated by a *small* number of white spots resembling gannets, which may have been gannet-like accretions of droppings on the ledges.

On 30 April 1942 a bomber of Coastal Command flew round Boreray and the Stacks, and took many exceptionally fine photographs in perfect weather. Among these was a 'vertical' taken from 9000 ft. exactly over the highest point of Boreray. An enlargement of this, on an approximate scale of 1 : 8970, and topographical notes made by J. Fisher on Boreray in 1939, were used to prepare a map illustrating the counts made on Boreray and the Stacks in all years.

The best existing map of St Kilda was made on the scale 1 : 10560 (6 in. to 1 mile) by J. Mathieson and A. M. Cockburn and published by the Ordnance Survey in 1928. Mathieson's trigonometrical points on Boreray are visible on the R.A.F. photograph so it was possible to collate the two and produce a sketch-map, Map 1. Map 2 is an outline derived from Map 1, to show the groups of gannets. Those familiar with Mathieson's map, made under difficult conditions, will see that, considering the nature of the landscape, it is accurate and useful. But the air photograph and the sketch from it show that Mathieson's outlines of Stac an Armin and Stac Lee were incorrect and, further, they show the outline and topography of the northern end of Boreray more realistically. This is very important for those who study gannets. For this reason Map 1 is published in full detail.

On three of the photographs taken on 30 April 1942 of Stac Lee, the gannets can be counted with the aid of a grid. Again, a sample showed that at 20 % of the nests both adults were present. There were, of course, no young present. Results were:

Rock	Group	Map ref.	No. counted	Approximate no. of pairs	
Stac Lee	S.E. face	13	3222	2578	
	Top table, photo. A	14	3289	2631	mean 2474
	Top table, photo. B		2895	2316	

Table 2. *Counts and estimates of the number of pairs of gannets on St Kilda*

Rock and Group	Map ref.	1902 J. Wigglesworth	1931 T. H. Harrisson	1939 (Blacker, Fisher, Huxley and Nicholson): Counted, Slowly	Counted, Rapidly	Estimated, 31 May, from sea, swell	Estimated, 2 June, from sea, calm, and 31 May, from land	Total, Min. taken as	Total, Max. taken as	Total, No. taken as	1941 Coastal Command photos. 31 Aug.	1942 Coastal Command photos. 30 Apr.	Map ref.
Stac an Armin:													
N.W. face	1	—	—	—	1,520	(2,500)	—	1,400	2,000	1,520	—	—	1
N.E. face	2	—	—	—			(1,000)				2,676	—	2
S.E. face	3	—	—	—	400	—	(500)	375	450	400		—	3
S.W. face	4	—	—	598	—	(1,500)	—	500	800	598	—	—	4
Totals		3,000	5,600					2,275	3,250	2,518			
Boreray:													
Geargo	5	—	—	—	750	—	—	700	1,000	750	962	—	5
Udraclete	6	—	—	915	—	—	—	900	930	915	—	—	6
E. side Na Roachan to Creagan na Rubhaig Bana	7	—	1440†‡	4,155	—	—	—	4,000	4,300	4,155	—	—	7
S. side Clagan na Ruskochan	8	—	—	61	—	—	—	60	65	61	—	—	8
W. side Clagan na Ruskochan and Clais na Runaich	9	—	880‡	—	800	(2,000)	—	1,400	1,800	1,550	598*	—	9
W. side Na Roachan	10	—	—	—	750						—	—	10
Mullach an Eilein	11	—	—	—	—	—	2,000	1,800	2,200	2,000	—	—	11
Totals		8,000	3,440					8,860	10,295	9,431			
Stac Lee:													
N. face	12	—	—	—	1,010	—	—	950	1,070	1,010	—	—	12
S.E. face	13	—	—	—	1,358	(2,000)	—	1,300	1,500	1,358	2,050	2,578	13
Top table	14	1,500	—	—	—	(5,000)	2,000	2,400	3,000	2,000	—	2,474	14
S.W. face	15	—	—	—	585		—			585	—	—	15
Totals		3,750	8,000					4,650	5,570	4,953			
Totals used		14,750 put at *c.* 15,000	17,040 est. at 16,500	5,729 (34 %)	7,173 (42 %)	—	4,000 (24 %)	15,785	19,115	16,902			

The figures in brackets were not used in the final totals, except indirectly, as an aid to deciding the probable maxima and minima; the main object in showing them is to demonstrate the tendency to overestimate, especially from a boat with a swell running.

* West side Clagan na Ruskochan only.
† Creagan na Rubhaig Bana only.
‡ By subtracting 20 % from Harrisson's figures for the numbers of birds.

The figures for the south-east face of Stac Lee suggest a further increase, but the remarks attached to the 1941 counts, concerning sampling and 'white spot' error, also apply to the 1942 figures. Allowance has also to be made for population decrease and nest deserting during the season, for the 1941 counts were made near the end of the season, and the 1942 counts at the very beginning.

The air photographs certainly do not indicate a decrease in the numbers of gannets anywhere on St Kilda; indeed, they hint that the population may be increasing. If new photographs are taken each year we should have a most valuable method of keeping in touch with developments in this most important of all gannet colonies.

Summary

1549: 'wyld foullis' paid in duties to owner.

1684: gannets nesting in the Hebrides.

1696: at least 800 taken Stac an Armin; 22,600 (erroneously) said to be eaten in all.

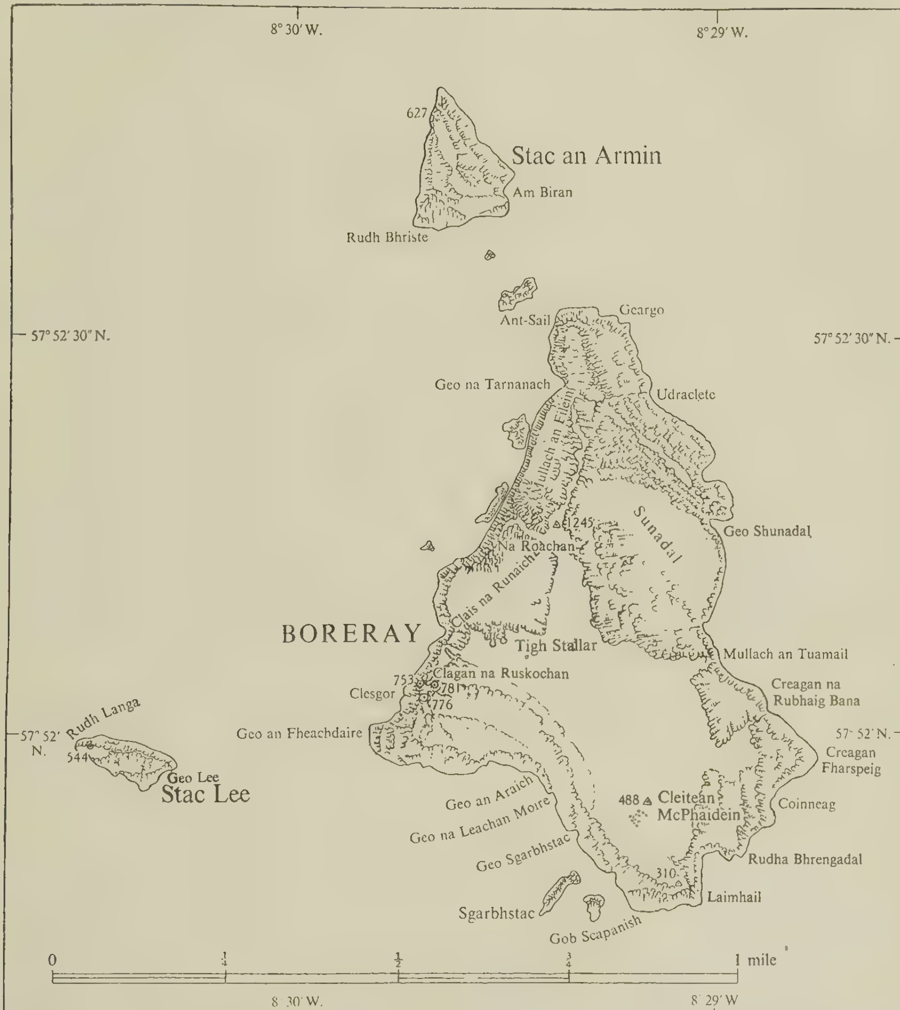
1697: Stac Lee stated to provide 5000, 6000 or 7000 gannets a year; Boreray, 'solan geese possess it for the most part'; Stac an Armin, 'abounds with Solan geese'.

1758: eggs taken Boreray and Stac an Armin only, young taken on these and on Stac Lee. 20,000 gannets (erroneously) said to be still taken annually.

c. 1786: 1200 said to be taken in one night.

Up to 1829: never more than 5000 young taken.

1829–43: never more than 2000 young taken.



Map 1. Sketch-map of Boreray, St Kilda, and its adjacent Stacs, drawn by James Fisher from a photograph taken on 30 April 1942 by an aircraft of Coastal Command, R.A.F., vertically above Boreray at a height of 9000 ft., and collated with the 6 in. to a mile map surveyed by John Mathieson and A. M. Cockburn and published by the Ordnance Survey in 1928. Approximate scale, 1:17,900. Heights in ft.

1840: all stacks occupied, some non-breeders present, *c.* 1600 young taken.

1841: *c.* 1120–1400 gannets taken; record of 15,000 gannets taken erroneous.

1847: 1100 gannets said to be taken in single night.

c. 1869: population estimated (not reliable) *c.* 25,000 pairs.

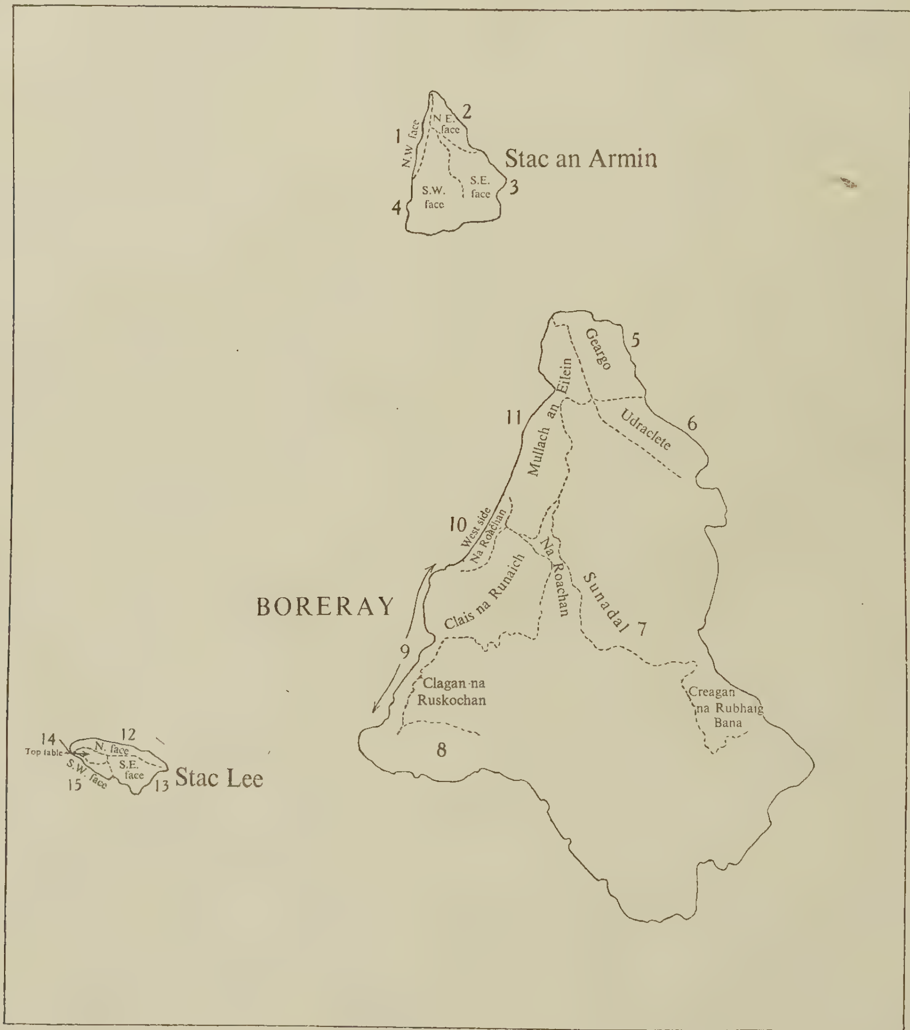
1930: man ceased to reside in St Kilda through the year, as from September.

1931: estimate *c.* 16,500 pairs.

1939: count (a quarter estimated) *c.* 16,900 pairs.

1941: probable increase on all three stacks.

1942: possible further increase on Stac Lee.



Map 2. Sketch-map of Boreray, St Kilda, and its adjacent Stacs showing the areas into which the cliffs were divided for counting the different parts of the gannet colony. Approximate scale 1 : 17,900.

1875, 1876: probably very few gannets taken.

1879: Stac an Armin and Stac Lee covered on slopes, summits and sides.

1884: breed in 'tens of thousands'.

1885: capture of 660 adults in two nights considered a great success.

1895: *c.* 3200 birds taken in all.

1902: only 300 taken, raids fallen into abeyance; reliable estimate 14,500–15,000 pairs.

1910: 600 adults taken, young no longer caught.

20. Rockall, North Atlantic, 150 miles west of St Kilda

One of the authors (75) has summarized the ornithological history of this remote rock, up to and including the observations from Coastal Command aircraft in the summer of 1941.

Gannets were present on the rock, but not breeding, in 1941 and in several previous years. Small numbers use it, simply as a resting place.

Crown copyright reserved *R.A.F. official photo*

Photo. 10. Sula Sgeir, 3 May 1941, approximately from the north-east. Greatest height 229 ft. The gannet colony is on the southern massif of the rock, which is altogether about half a mile long. Reproduced by permission of Coastal Command, Royal Air Force.

Copyright *J. Fisher*

Photo. 11. Sula Sgeir, 4 June 1939, approximately from the south-east. Height 229 ft. Nearly all the gannet cliffs are visible from Sròn na Lice on the left to Sgeir an Teampuill on the right, excluding Pairc ás Iàr. In 1939 the population was about 4000 breeding pairs.

Copyright *J. Fisher*

Photo. 12. Gannets in flight over Sula Sgeir, 4 June 1939.

Copyright *J. Fisher*

Photo. 13. Sule Stack, 24 May 1939, approximately from the south-west. Height *c.* 125 ft. The highest point visible in the photograph is part of the main, northern massif on which all but 100 of the *c.* 3500 pairs were breeding in 1939. The birds visible in the right foreground are some of the considerable number not occupying nest-sites.

Summary

Present on or near Rockall 1810.

Present on the rock but not breeding 1887, *c.* 1894, 1896 (10 birds), 1921.

Present but not breeding 1941 (1 on rock 19 June; 15 near rock 23 June; 1 on top and *c.* 6 near rock 3 July; none 18 July, 7 August).

21. Sula Sgeir, Outer Hebrides, Ross

Monro (**154**) gives us the first account of this gannetry (1549). He says: 'This ile is full of wylde foulis, and quhen foulis has ther birdes, men out of the parochin of Nesse in Lewis use to sail ther, and to stay ther seven or aught dayes, and to fetch hame with them their boitt full of dray wild foulis, with wyld foulis fedders.' The rest of his account certainly refers to the eider duck.

Not only is this the first reference to the gannet here, but it is also the first reference to the annual boat journey that the men from Ness (Barvas parish), about 50 miles away, still make almost annually in an open boat to collect young gannets for food (human food, dog food and cattle food in winter). To this day (**267**) the September expedition is made in a 40 ft. skeffa, a direct descendant of the old Norse galley and the only boat of its type remaining.

In 1597 Moniepennie (**153**) says: 'sea fowles lay egges there, and doe hatch. They of Leogus, next neighbours unto it, get great profit thereby'; but his account (as are many of his accounts) was probably copied from Monro.

In 1819 (**40, 218**) Sula Sgeir is mentioned as a great gannet resort. In 1860 T. S. Muir (**40, 218**) visited Sula Sgeir, but says little about the gannets.

Writing in 1869, Elwes (**66**) states: 'this rock is still visited annually by a boat from Ness, which goes in September, for the sake of the down and feathers of the young gannets, at that time nearly ready to fly. Several thousands are usually killed, and are considered very good eating, as they are extremely fat and as large as the old ones.'

In 1871 Gray (**87**) just mentions the colony. In June 1883 Swinburne (**218**) visited Sula Sgeir and states: 'in the breeding season...sometimes 2000–2500, or even 3000 young birds may be taken.' Some years before this the boat of the men from Ness was wrecked in landing there, in June, and the men were stranded for some weeks. Harvie-Brown (**40**) visited the rock on 19 and 20 June 1887, just after the Ness men had made their annual raid; only *c.* 100 gannets occupied an area of Sron na Lice where Stewart (**213**) photographed 452 in 1932 and 541 in 1937. Harvie-Brown records that at that time Sula Sgeir exceeded both the Bass Rock and Ailsa Craig in numbers, so there seems to be some justification for recording it then as over 5000 pairs. (An estimate of the Bass Rock population in 1869 (probably inaccurate) gave *c.* 6000 pairs in 1869. In 1871 and 1872 estimates (of little value) gave *c.* 10,000 pairs; in 1873 the Bass gannets were increasing, but though there was less molestation in 1885 the colony decreased to 3000 pairs in 1904. In 1869 an unreliable authority gave the Ailsa population as *c.* 6000 pairs; by 1905 a figure of possibly *c.* 3250 was recorded.) Harvie-Brown also records that in 1884 the Ness men took 2800 birds in 3 days.

On about 21 June 1891 Newton & Evans (**248*a***) visited Sula Sgeir (but did not land). Newton writes: 'I think there must be more gannets there than on Stack (perhaps twice as many).' Newton (**95**) had visited Sule Stack in the previous year.

In *c.* 1892, as Norman MacLean, one of the gannet hunters, told Gordon (**83**), it was necessary to take all gannets possible, with the aid of ropes. The population in this year was said by him to be half what it was in 1937. Judging by the figures for young taken in 1884 and 1898, compared with those taken in 1937, this statement cannot be taken seriously, and Gordon's case against the protection of gannets on this rock cannot rest on this hearsay evidence. As we shall show, in Part II of this paper the case itself has some weight, despite the unreliability of the statements of some of its advocates.

Gurney (**95**) records that in 1898 2500 were taken, and in 1912 2200. A raid was also made in 1911. Basing his figures on the number of young taken in 1884, Gurney computed the population at 4000 pairs. (The 1869 authority previously quoted (and misquoted by Hay (**102**) in 1881) gave us (**183**) the first computation of the gannet population of Sula Sgeir—150,000 pairs—which is why we regard his figures with some suspicion.) Stewart (**215**) criticizes Gurney's computation and points out that (as is clear from the date of Harvie-Brown's visit in 1887) the Ness men did not confine themselves to taking young birds, but took adults and eggs as well. Stewart produces very sound reasoning to support the fact that in 1884 the population was not of the order of 4000, but more like 7000 pairs.

According to Stewart (**213**) 1100 young were taken in 1915, and during the 1914–18 war shell-fire practice by warships made a large number of gannets desert the rock. From then until 1931 we have no information.

In August 1931 Harrisson (**100**), who visited North Rona at that time to study the Leach's fork-tailed petrels, saw Sula Sgeir and writes: 'I made a rough long-distance estimate of 9000 adults on Sulisgeir, concentrated on the south and south-east cliffs.' It is probable that Harrisson's estimate was made from a considerable distance, perhaps as long as several miles. In this year Stewart (**213**) records that 2000 were killed by the men from Ness in Lewis.

In 1932 Stewart (**212**) stayed on the rock for 36 hr. on 23–24 July. He attempted no accurate estimate, but stated that 6500 adults were present. Wynne-Edwards *et al.* (**65**) construed this as *c.* 5000

breeding pairs. Stewart indicated the northern limit of the colony on the 6 in. Ordnance Survey map.

In 1933 (**213**) 2000 were again killed by the men from Ness. In 1934 only 1400 were taken, as illness curtailed their visit. In 1935 there was no visit owing to bad weather. In 1936 2060 were taken by nine men in a fortnight. In 1937 *c.* 2000 were killed, according to Stewart (**213**), and, according to Gordon (**83**), six tons were taken. Six tons would represent about 1800 gannets. The Ness men spent a fortnight on the rock in September. Gordon (**83**) states that this raid was led by Murdo MacKay, with Norman MacLean as second, and seven others. MacLean told him that no adults or small young were killed, and that, in his reckoning, 4000 young birds were left undisturbed, while several hundred saved themselves by flight. This would make the population over 6000 pairs. We accept Stewart's figure; not this. MacLean said the population had increased 100 % since *c.* 1892.

Stewart's second visit to Sula Sgeir (**213**) was on 5 August 1937. He made a count of the colony, recording the total number of breeding pairs as 4418. This is compared in detail with the 1939 total in a later paragraph. Stewart again marked the limits of the colony on a map.

In 1938 about 2000 young gannets were taken (**16**). This was 'considered very good'. The crew were out for three weeks, and were at least ten in number. 'The men expressed the view that the gannets are increasing, and had not been so numerous at any time in the past 20 years.' A correspondent in the *Stornoway Gazette* for this year (unfortunately the cutting in our possession is not dated) also states that 'there were hundreds more this year than ever before'. In a sober analysis of the situation all these must be treated as interested parties.

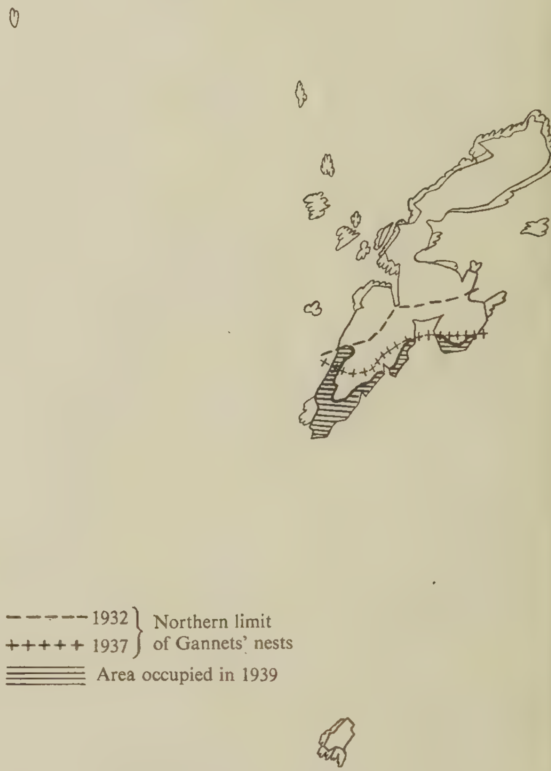
The 1939 party arrived in the auxiliary ketch *Escape* in the early afternoon of 4 June. There was a heavy swell running and it was with some difficulty (and partial immersion) that Fisher was landed. Unfortunately only about 15 minutes could be spent on the rock since the wind increased. The 1939 estimate is, thus, based on rapid counts from the land, with the gaps filled in by an eye survey from the sea; owing to the swell it was impossible to use glasses.

Compared with Stewart's results for 1937, the count is as follows (number of pairs in occupation of nest sites):

	1937	1939
Sgeir an Teampuill	508	450
Meagh Cich	2028	350
Creag Trithaiga		1650
Pairc ás Iàr	1022	700
South end near summit	86	820
Srõn na Lice	774	
Totals	4418	3970

At the end of June 1939 Dr F. Fraser Darling attempted to land in a very heavy swell (**267**). He was unable to do so, but estimated from the sea that *c.* 4000 pairs were present. This estimate, quite independent of ours, is remarkably close. Dr Fraser Darling joined the gannet-counting party on Ailsa Craig in April 1939 and has therefore had some experience in counting and estimating the numbers of gannets.

On 3 August 1939 Mr Robert Atkinson (**255**) made a successful landing and stayed on the rock for 24 hr. He was able to complete the picture of the



Map 3. Sula Sgeir. Sketch, based upon Ordnance Survey map by permission of the Controller of H.M. Stationery Office, by R. Atkinson (3 August 1939) and J. Fisher (4 June 1939), showing the area occupied by gannets in 1939, compared with the areas recorded by Malcolm Stewart as occupied in 1932 and 1937.

1939 situation by redrawing the map of the colony's limits. Map 3 shows his results, compared with those of Stewart in 1932 and 1937.

From the counts and the map it is quite evident that there has been a steady decrease of the population of the Sula Sgeir colony since 1932. (The only ornithologist who still holds that the population of Sula Sgeir is increasing is Gordon (**83**) who has relied on the *opinions* of interested parties. This view is not in accordance with the facts.) This raises several points which will be more fully discussed in Part 2 of this paper.

The men from Ness were prevented from making a raid in 1939 by bad weather, according to Stewart (**303**), but according to Gordon (**83**) were on the rock when war broke out on 3 September.

Summary

Breeding, birds taken by men from Ness 1549, 1597.

Great gannet resort 1819; gannets present 1860.

'Several thousand' birds usually killed annually 1869, and ridiculous estimate 150,000 pairs.

Mentioned 1871.

Ness men's raiding boat wrecked in June some years before 1883; average 2000–2500 young, maximum 3000, taken annually by 1883.

2800 birds taken in 3 days—population *c.* 7000 pairs—1884.

Over 5000 pairs, adults taken in June 1887.

'Perhaps twice as many' as on Sule Stack, 1891; young taken *c.* 1892; 2500 birds taken 1898.

Young taken 1911; 2200 taken 1912.

1100 young taken 1915; numbers deserted owing to gunnery practice 1914–18.

2000 birds killed, unreliable estimate *c.* 9000 adults on rock 1931.

c. 5000 breeding pairs 1932; 2000 birds killed 1933; 1400 taken 1934; none taken 1935; 2060 taken 1936.

1800–2000 killed 1937, 4418 breeding pairs, area occupied smaller than in 1932.

c. 2000 gannets taken 1938.

Birds taken 1939, 3970 breeding pairs and occupied area still further reduced.

22. North Rona, Outer Hebrides, Ross

Swinburne (**218**), who visited North Rona in 1883, says that gannets are said to have bred there, but there is no further information on this subject, and none of the many naturalists who have visited this island since that date has ever suspected gannets to be breeding; thus Barrington in 1885 and Harvie-Brown (**39**) in 1886 only observed the gannet at sea.

Summary

Breeding not proved by 1883; certainly not breeding since.

23. Sule Stack, Orkney

The first reference to gannets at this colony must be that of Sibbald (**201**) who wrote, in 1710, that they were found 'in a desart isle belonging to Orkney'. Pennant mentions the colony by name in 1776 (**184**). Low (**137**), who died in 1795, mentions Sule Stack as the nearest breeding place to Orkney, and states that 'some time ago' it was raided from Orkney, and a great quantity of young taken.

Neill (**169**), writing in 1806, mentions that 'several years ago' the raiding vessel was wrecked (either on Sule Skerry or Sule Stack—both were raided, the former for seals). In 1806 a new vessel was equipped and the gannets having 'enjoyed a jubilee', were 'found to have multiplied to an inconceivable degree'. It is clear from Neill's text that he cannot have made a personal visit and his remarks on population change must be treated with reserve.

The colony is mentioned by Baikie & Heddle (**25**) —'breeds in great numbers', *c.* 1848—and by Preyer & Zirkel (**185**), who passed it on their way to Iceland in 1860. In 1869 Elwes (**66**) recorded it as a large colony, and Mr M'Donald, the commander of H.M. Cruiser *Vigilant*, told Lord Caithness that 50,000 birds bred there (**183**). The wildness of this gentleman's estimates has already been commented upon. Gray (**87**) mentions the colony in 1871.

In 1887 Harvie-Brown visited Sule Stack and found the entire summit densely populated with gannets, and a large proportion of immature birds present (**45**). He records that the colony was, at that period, raided (almost certainly by the men from Ness), but not as persistently as the colony on Sula Sgeir.

On 28 June 1890 Messrs Newton and Evans visited the rock (**95**) and also commented on the large number of immature birds present. When they visited Sula Sgeir in the following year (**248***a*) Newton thought that there were 'perhaps twice as many' there as on Sule Stack. Stewart (**215**) shows that the Sula Sgeir population in 1884 was probably about 7000 pairs, which gives *c.* 3500 for Sule Stack —a likely figure for this very constant colony.

By 1902 J. Tomison (**225**) was noting arrival and departure dates, and the fact that the rock was simply covered at its top with gannets.

Gurney (**95**) was told by N. A. McIntosh, principal lighthouse-keeper at the neighbouring island of Sule Skerry, that the population was of the order of 8000–10,000 birds. Gurney put the total at *c.* 4000 pairs. McIntosh also told him that in 1903 or 1904 a boat went to raid the colony from Ness, but got windbound on the Sutherlandshire coast; and the men were not going to the Stack any more, having had enough of it. McIntosh stated that on these raids, which were made in August, never more than 1000 were taken, as only a small part of the rock was accessible. In 1911, Gurney also records, the colony was raided from Ness for young gannets; the Lewis men had changed their minds.

On 17 May, and 19 and 21 June 1914, the Duchess of Bedford (**27, 96**) visited Sule Stack in her yacht. On 19 June, when she steamed and rowed around, about 5000 (certainly less than 6000) adult birds were present on the rock. Only the upper third (with Stewart, we would suggest the upper half) of the North Rock was occupied, and on the South Rock the Duchess of Bedford recorded about 6 nests. She considered that 1 in 6 of the total population was immature. When she visited the Stack again on 21 June she was quite satisfied with her former

estimate of 5000 birds. Wynne-Edwards *et al.* (**65**) construe this as 4000 pairs.

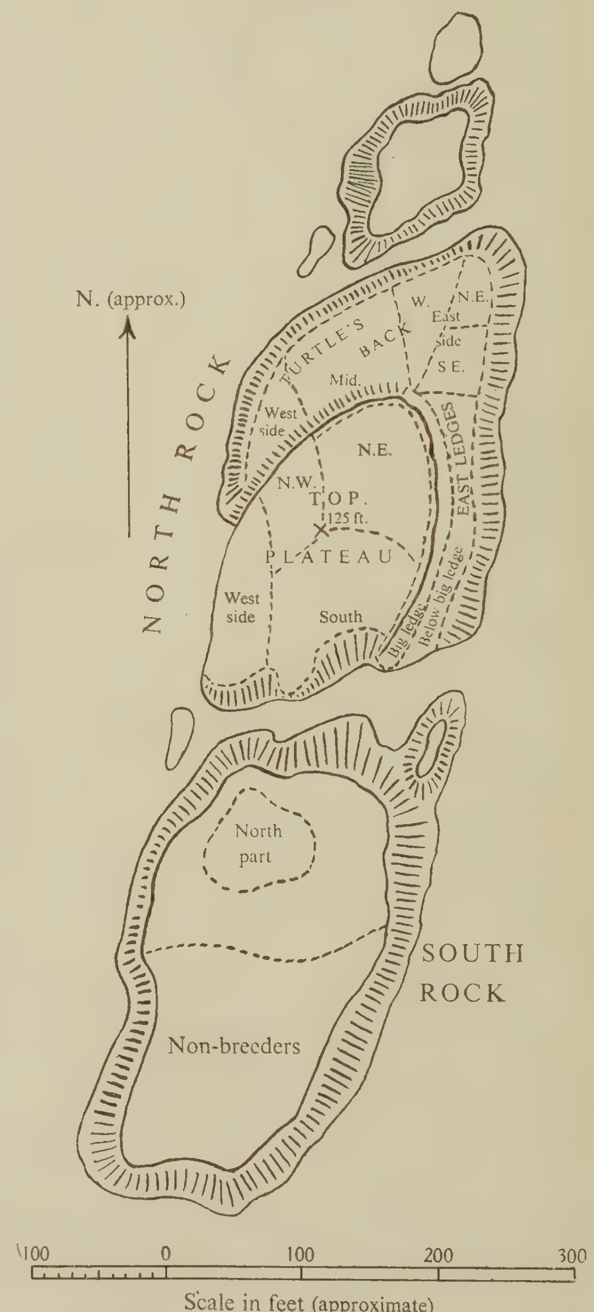
The anonymous contributor to the *Stornoway Gazette and West Coast Advertiser* in 1938 states that the Ness men used to take 1200 birds annually, but that none had been taken since 1932, and further states (quite erroneously) that 'the rock is almost deserted of gannets'. This statement was put forward to prove that changes in the population of gannets were quite independent of the Ness men's raids.

Stewart's landing on the morning of 31 July 1937 (**213**) was, as he says, no mean feat. He discovered that a very large number of non-breeders was present. His assessment of the population was based very largely on photographs, and the reader is referred to his most interesting paper for the arguments on which he based his final figure of 3418 breeding pairs, or roughly 3500. *c.* 118 pairs were breeding on the South Rock, though, he admits, this may have been an overestimate (we found 100 pairs here in 1939). Stewart also states that 'it is not thought that any nestlings have been taken for food for many years'.

On 24 May 1939 the *Escape* visited Sule Stack. The swell prohibited landing, but the ketch cruised round the rock for nearly 2 hr. while J. Fisher, J. S. Huxley and E. M. Nicholson made direct counts, which, with the addition of counts from photographs, give what we consider to be a reasonably accurate idea of the number of occupied nest-sites. The groups correspond to the areas on our sketch-map (Map 4) which, made by one of us from photographs and rough bearings, is, as far as we know, the only map published of this rock. Sule Stack and Sule Skerry are among the very few parts of Britain not covered by the Ordnance Survey; for a map of the former see Stewart (**214**). Our counts are as follows (no. of pairs):

NORTH ROCK		
Turtle's Back		
East Side:		
S.E.	275	Direct count
N.E.	145	,,
W.	300	,,
Mid	500	,,
West Side / Top Plateau / N.W.	650	,,
West Side	255	From photograph
South	250	,,
N.E.	400	Direct count
East Ledges		
Big Ledge	150	,,
Below Big Ledge	465	Direct count, 462 from photograph
SOUTH ROCK		
North Part (highest)	100	Direct count
TOTAL	3490	

In using photographs for counting we had the advantage over Stewart in that young birds were not yet hatched—whereas at the date when Stewart made his counts they were liable to be confused with adults in distant photographic view. On the other



Map 4. Sketch-map of Sule Stack, pertaining to Stromness, Orkney, lat. 59° 2′ N., long. 4° 30′ W. Made by James Fisher from photographs and rough compass bearings taken on 24 May 1939, from the auxiliary ketch *Escape* (owner and navigator, D. Robertson). The grouping of the gannets for counting is delineated.

hand, Stewart landed and got right among the gannets.

It can be seen that our counts and Stewart's correspond very closely. Speaking in rather wide terms, Sule Stack is full up. There is room for more breeding gannets perhaps only on parts of the South Rock now usually occupied by non-breeders; otherwise every available ledge is occupied, as far down as the swell will permit. The estimates of *c.* 4000 pairs in 1904 and 1914 may have been too high.

We noted large numbers of non-breeders. Certainly up to 500 birds were in immature plumage; being attached to no definite site, these birds were not easy to count. The non-breeders congregated particularly on the smooth southerly turtle-back of the South Rock.

Summary

First mentioned 1710; mentioned again 1776.

Raided for young birds from Orkney some time before 1795.

Raiding ship wrecked *c.* 1800; raid in 1806, when great increase alleged.

Mentioned 1860; recorded as 'large colony' 1869 and population estimated quite erroneously at 25,000 pairs.

Mentioned 1871.

Summit densely populated 1887, many immature birds, colony still raided (probably from Ness, Lewis) at this period.

Large number of immature birds present at colony, possibly *c.* 3500 breeding pairs 1890.

Rock 'simply covered' 1902; attempted raid from Ness 1903 or 1904; up to 1000 birds taken in some years previous to this.

c. 4000 pairs estimated *c.* 1904.

Young taken 1911; *c.* 4000 pairs estimated 1914.

1200 birds said to be taken in some years up to 1932, since when no further raids.

3418 breeding pairs 1937, many immature birds and non-breeders.

3490 breeding pairs 1939, *c.* 500 immature birds present.

24. Copinsay, Orkney

In 1907 or 1908 a pair of gannets lived about the cliffs on the east side of Copinsay for a short time during the nesting season (**20**); and in about 1911 a pair is reported to have contemplated nesting on Copinsay or on the Horse of Copinsay, rather over a mile away. A report (**19**) of nesting on the Horse of Copinsay in 1914 was later shown to be erroneous. No birds were present in 1915.

Mr A. McGaw, late principal lighthouse-keeper at Ailsa Craig, was stationed on Copinsay from 1924 to 1927. He informed us that in 1925 or 1926 (**295**) a pair of gannets carried material and built a nest 200–300 yd. north of the lighthouse. One bird died on the nest, but the other stayed all the season. No other gannets were present. No birds had been noted in the previous season; nor did any return in the following year.

Summary

Attempt at breeding not proved, 1 pair present 1907 or 1908.

Possible attempt at breeding, 1 pair present *c.* 1911.

No birds present 1914, 1915, 1924.

Unsuccessful attempt at breeding, 1 pair present 1925 or 1926.

No birds present 1927.

25. Noss, Shetland

To the account of this colony already published by Fisher & Venables (**77**) we have the following to add:

No birds were present in 1909 (**263**), and in 1936 the birds were 'like snow'. In 1939 J. S. Huxley and J. Fisher took counts on 20 and 21 May. Compared with the estimate in 1937 and the count in 1938, these counts are (number of pairs):

	1937	1938	1939 J. F.	1939 J. H.	1939 Mean
A. N. face of Noup (from Point of Heogatoug)	431	460	576	575	576
Dead ground on Noup, counted from boat		35	72	—	72
B. S. face of Noup (from Rumble Wick): Group 1	206	222	342	—	342
Group 2		60			
C. Rumble Wick (from Noup): Group 1	276	113	116	126	121
Group 2		390	333	335	334
Group 3		159	168	—	168
Group 4		169	217	217	217
Totals	913	1518	—	—	1830

In 1937 the estimate was made by the alighting method. It was probably too low—the figure for the groups in C particularly. In 1938 and 1939 direct counts were made with field glasses.

It can thus be seen that the numbers of gannets are still increasing fairly evenly on all parts of the colony. The increase in 1939 over the 1938 total was one of 20·6 %. An increase of 25 % would mean that colonization must certainly have taken place, and the observed figure shows it to have been a practical certainty.

Summary

No birds present 1909.

Birds first showed interest 1911 or 1912; one pair

bred 1914; 4 pairs bred 1915; 3 young reared 1918; 5 pairs bred 1919; 10 pairs bred 1920.

c. 200 pairs 1930 or 1931; *c.* 800 pairs 1934 or 1935; birds 'like snow' 1936; *c.* 913 (+?) pairs 1937; 1518 pairs 1938; 1830 pairs 1939.

26. Hermaness, Shetland

As with Noss, a recent summary of the history of this colony to 1938 has been published (**76**). The 'North Stack', mentioned by Saxby (**199**) and Gurney (**95**), should be identified with the Out Stack, which lies beyond the Muckle Flugga and is the northernmost rock of Great Britain. Both these authorities agree that gannets have never bred there, and the present flourishing colony south of the Muckle Flugga shows no sign of spreading to the Out Stack, or to the Muckle Flugga itself.

In 1939 the colony was visited and counted by Malcolm Stewart (**303**). From his experience in this year he considers that the figure of 653 pairs for the whole of Vesta Skerry in 1938 was an underestimate, probably of the order of 150 pairs. Stewart's counts on 11, 12 and 13 July 1939 showed 2611 pairs in occupation of nest-sites, distributed as follows:

It can be seen that there was a remarkable increase in 1939 throughout the colony. Only part C of the Neap Group (for diagram of parts see (**76**)) had a smaller total than in 1938. The increase of 566 pairs in 1939 represents 22·8 % of the previous year's total. The greatest increase is on Vesta Skerry, whence a count of 653 pairs was published for 1938. In 1939 there were 967 pairs, an increase of 314. Stewart, who took part in the 1938 counts, suggests that a large group of gannets nesting in a hollow part of the top of the rock on the eastward side may have been ignored, at least partly, in 1938. This may be true; but the main increase seems to have taken place on the west side, where only 146 pairs were present in 1938, as opposed to 429 in 1939. We do not feel that we can accept Stewart's suggestion, and add an arbitrary 150 pairs to the 1938 total of the 'east side and top' of Vesta Skerry. Though they were much foreshortened, the gannets in the hollow were visible to J. Fisher when he did his count from the sea in 1938, and if any serious inaccuracy resulted it may have been due as much to the birds' foreshortening as to their invisibility.

It is a practical certainty that colonization is continuing at Hermaness.

		1939		1938
		Direct count	Total taken as	For comparison
Vesta Skerry	E. and Top	538		
	W.	429		
	Total		967	653
Humla Stack	From Clingra	162		
	N.	3		
	From sea	20		
	Total		185	156
Burra Stack	From Clingra	44		
	From Humla Stack	38		
	From sea	235		
	Total		317	234
Humla Houl	From Clingra	147		
	From Humla Stack	59		
	Total		206	192
Neap				
A (Neapna Stack)	N. from B	157		
	S. from Saito	189		
	Total		346	341
B	From Saito	330		
	From sea	50		
	Total		380	274
C	From above	95		
	From sea, total, 2nd count	95		
	Ground dead from above, visible from sea	7		
	Total		98	102
D	From Saito	33		
	From sea	6		
	Total		39	27
E	From Saito	73	73	66
Totals			2611	2045

Summary

Not breeding 1874, 1913.

Colony established Vesta Skerry 1917.

Had spread probably to Burra Stack, at least 109 pairs, by 1920.

Estimate 1000 pairs probably too high 1928.

Had spread to Humla Houl, the Neap and Neapna Stack by 1932.

May have been over 600 pairs 1934; *c.* 1000 pairs 1935.

Had spread to Humla Stack, count of 2045 pairs 1938.

Count of 2611 pairs 1939.

27. Myggenaes Holm, Faeroes

The history of this colony up to 1937 has been published in some detail by Vevers and Evans (**235**). Vevers visited Myggenaes again in 1938 and 1939, in the latter year with L. S. V. Venables, and their counts were as follows (number of pairs):

		1937 Vevers	1937 Evans	1937 Mean	1938 Vevers	1939 Vevers	1939 Venables	1939 Mean
West end, Myggenaes		1	1	1	1	1	1	1
Myggenaes Holm: A		120	119	119·5	119	67	65	66
B		209	209	209	222	93	96	94·5
C		250	257	253·5	261	348	344	346
D		28	28	28	27	23	23	23
E	(2 counts each)	186 184	192 182	186	174	254	247	250·5
F		217	211	214	223	179	185	182
G		218	224	221	226	197 (G and H)	191 (G and H)	194 (G and H)
H		35	35	35	39			
S.W. cliff		0	0	0	0	60	62	61
Píkarsdrangur	(2 counts each)	116 110	122 118	116·5	126	97	88	92·5
Flatidrangur		232	232	232	227	164	160	162
Totals				1615·5	1645			1472·5

Summary

Colony known 1673.

200 adults and 200 young killed 1782, 1800; human population of Myggenaes 75 in 1801.

300 adults and 600 young killed 1862; breeding 1872; estimate 750 pairs 1892.

Human population 179 in 1925; gannets breeding 1926; estimate 750 pairs 1928.

Estimate *c.* 900 pairs 1935 and catches in recent years *c.* 450 adults and 850 young; 1615 pairs 1937 and *c.* 700 young, no adults taken; 1645 pairs 1938; 1473 pairs 1939.

Tindholmur, Faeroes

On 14 April 1942 K. Williamson (**308**), stationed then in Faeroes, wrote to one of us: 'I was informed recently that gannets nest on Tindholmur, an islet not far distant from the Myggenaesholmur colony and whilst I very much doubt this the mere fact that they have been seen ashore there is interesting enough to call for further examination.'

Mr Williamson was asked to conduct this further examination personally, if he could; but we have not yet heard whether he was able to get to this rock. Meanwhile, we cannot quite include it in our list of past, present or possible colonies.

(g) ICELAND GROUP

The only mention of the gannet in early Icelandic literature is to be found in Snorri's Edda (**217**), where the name *súla* (modern Icelandic *hafsúla*—gannet) occurs.

28. Westmann Islands

Gizur Pjetursson (**115**), in the Westmanns from 1687 to 1713, said 'the gannet breeds in these four islands, Súlnasker, Hellisey, Geldungasker and Brandur, but not in the others'.

Olafsen (**178**), from visits between 1752 and 1764, gave a description of the capture of the gannet by the Icelanders and records it as breeding on 'Suluklettur, a rock among the Westmann Isles', evidently the modern Súlnasker.

Faber (**71**) recorded the gannet as breeding on 'three isolated skerries in the Westmann Isles, namely Brandten, Suluskjer and Geirfuglaskjer'. He visited Brandten (Brandur) himself. 'Geirfuglaskjer' was probably an error for Geldungur, since the former rock is almost certainly too low to have supported a gannet colony. Faber visited Iceland between 1819 and 1821.

Jón Austmann (**115**), who, like Pjetursson, was a pastor on the Westmann Islands, writing in about 1839, said that gannets were then nesting on Súlnasker, Hellisey, Brandur and Geldungur, and pointed out the mistake of Olafsen and Poulsen in stating that it only nested on Súlnasker; Austmann recorded that about 260 pairs nested on the summit of Súlnasker.

Preyer & Zirkel (**185**), who visited Iceland in 1860, evidently follow earlier sources in recording the gannet as common in the Westmann Islands.

In 1862 Thordersen (**224**) recorded that the islanders usually took from 400 to 500 gannets from Súlnasker every year.

In 1895 Gröndal (**91**) records the gannet as common in the Westmanns; in 1896 Jónsson (**116**) stated that numerous gannets nested in four of the outer isles of the Westmanns, but gave no further details. Slater, in 1901 (**204**) simply records the gannet as breeding in these islands. In about 1903 Hantzsch (**99**) only records (in error) Súlnasker as a breeding place of the gannet in the Westmann Islands.

Annandale (**5, 6, 7**) describes a visit to Súlnasker in 1898. 560 young were killed on Súlnasker in September of this year, and 662 in the whole of the year, according to him; but according to E. Gurney (**95**), his companion, 562 were killed in all, 440 on Súlnasker, 60 on Geldungur and 62 on Brandur. It is unfortunate that Annandale should have omitted all mention of the last two breeding places, and of Hellisey, from his own published accounts. An egg in the Wolley collection catalogued Súlnasker, Westmanns, 15 June 1899 (**173**) may have been taken by Annandale or E. Gurney in 1898.

From a consideration of the observations of Annandale and others, J. H. Gurney (**95**) proposed an estimate of 4000 breeding gannets for the Westmann Islands as a whole.

Nielsen (**175**) mentions the fact that two Englishmen had visited the colony some years previous to 1919, and had estimated that there were 5000 breeding pairs. (He may *possibly* have meant the visit of Annandale and Gurney in 1898, though it has not been recorded, in any literature that we can find, that they made the estimate here quoted.) On the grounds that between 500 and 1000 young gannets were killed annually, Nielsen himself, writing in 1919, considered the colony to be considerably larger than 5000 pairs.

In 1927 Hachisuka (**97**) mentions the gannet as breeding in the Westmann Islands, but gives no details.

Roberts (**189, 190**) visited the Westmann gannet rocks in 1932 and has published an interesting description of his counts. He concluded that the Westmann colony then held about 3900 breeding pairs. Lockley & Salmon (**134**) have criticized Roberts's methods of computing the total population from the counts obtained, and have suggested a modified population total (see later).

Roberts (**189**) also gives the official figures of young gannets captured on the Westmanns between the years 1913 and 1930. In this paper, these are given in the summary to this colony. It would be unwise to make any generalizations from these figures, which refer almost entirely to birds killed on Súlnasker, since the numbers vary according to the time allowed by weather conditions to the bird-catchers on any one trip; also, though the figures are official returns, they are not necessarily accurate. Certain of the islanders admitted in conversation (**306**, July 1939) that they never acknowledge the full number taken, since they are taxed on all those birds from which they may derive income. Most of the gannets caught in Iceland nowadays are sold as food for silver foxes.

Wynne-Edwards *et al.* (**65**) compute the number of breeding pairs on the four rocks occupied as 4000 in 1935, making use of the modification of Roberts's 1932 figure suggested by Lockley & Salmon (**134**) and the observations made by Lockley at Brandur and Hellisey in June, 1935. Lockley (**132**) found 317 nests on Brandur and estimated 2600 nests on Hellisey.

The four rocks, Brandur, Hellisey, Geldungur and Súlnasker were visited by H. G. Vevers, F. C. Evans and W. G. Alexander on 2 and 3 July 1939, and careful counts were made of the numbers of breeding pairs on each. A landing was made on Brandur, where a few pair snest on the upper slopes, and on Súlnasker, where many birds nest on the flat top.

The nature of the cliffs and the relatively well-spaced distribution of the nests on Súlnasker and the other rocks allowed each section to be split up into a large number of small groups for purposes of counting. In the following list the smaller groups have been added together, but where possible the total numbers of nests on the larger cliff-faces have been kept separate. The count for the top plateau of Súlnasker is a count of all nests, and it is now almost certain that about 200 of these were unoccupied at the time. In support of this Thorsteinn Einarsson (**274**), who visited Súlnasker in 1940, found only 523 actual nesting pairs on the summit, although there were 781 nests there. The numbers of nests are as follows (pairs in 1932 and 1935 for comparison):

	1932*	1935†	1939	1940‡
Brandur				
N.N.W. upper slopes	—	—	11	—
N.N.W. cliff	—	—	227	—
N. and N.N.E.	—	—	229	—
Total	390	317	467	—
Hellisey				
S.	—	—	47	—
W.	—	—	266	—
N.W.	—	—	350	—
N.N.W.	—	—	268	—
N.	—	—	702	—
N. (upper part)	—	—	70§	—
Total	1961	2600§	1703	—
Geldungur				
Main part	—	—	529	—
Part of main part	—	—	60§	—
Total	190	—	589	—
Súlnasker				
N.	—	—	299	—
W.	—	—	515	—
Top plateau	—	—	786	781
Total	973	—	1600	—
Grand total	3514	4000§	4359	—

* Roberts's figure for the number of birds seen, with 5 % subtracted to give the number of nests, as suggested by Lockley & Salmon (**134**).

† Lockley's count and estimate.

‡ Th. Einarsson. § Estimated.

The total of 4359 nests in the Westmann colony in 1939 suggests a recent progressive trend towards increase.

Summary

Breeding Brandur, Súlnasker, Geldungur and Hellisey *c.* 1700.

Erroneously recorded breeding only Súlnasker between 1752 and 1764.

Breeding Brandur, Súlnasker, Geldungur (probably also Hellisey, omitted in error?) *c.* 1820.

Breeding all four stacks, *c.* 260 nests top Súlnasker *c.* 1839.

Breeding 1860; 400–500 taken from Súlnasker years *c.* 1862.

Breeding 1895; numerous gannets nesting four stacks 1896.

Estimate *c.* 2000 pairs, 562 or 662 young taken 1898.

Breeding *c.* 1901, *c.* 1903.

480 young taken 1913; 363, 1914; 427, 1915; 526, 1916; 162, 1917; 159, 1918; 228, 1919 and estimate *c.* 5000 pairs about this year; 480 young taken 1920.

384 young taken 1921; 668, 1922; 376, 1924; 368, 1925; 656, 1926; 864, 1927; 824, 1928; 632, 1929; 536, 1930.

Estimate 3514 pairs 1932; estimate 4000 pairs 1935; count 4359 pairs 1939; 781 nests top plateau Súlnasker hints no great change in population 1940.

29. Eldey

The early history of the large gannet colony on Eldey (the Mealsack) is obscured by the lack of knowledge regarding Eldey itself and the neighbouring rocks, Eldeyardrangur, Geirfuglasker and Geirfugladrangur. These four rocks lie to the south-west of Cape Reykjanes, and are generally referred to as 'Fugleskaererne' or the 'Bird Skerries'. They are volcanic in origin and are the remnant of a previously more extensive archipelago.

Between 1752 and 1764 Olafsen(**178**) records breeding at 'Fugleskiaer, 6 miles south from Reykenaes', which must refer to Eldey itself, the largest and most northerly of the Bird Skerries, which lies 15 English miles south-west of Cape Reykjanes. Between 1819 and 1821 Faber(**71**) records the gannet as breeding on 'the two Bird Skerries to the south-west, namely Mealsack and Geirfuglaskjär'. In another place in the same paper Faber describes a visit to the Bird Skerries in the summer of 1821, and says that the upper surface of *one* of them was covered with breeding gannets and guillemots.

At the present time gannets nest only on Eldey. There is, however, a possibility that Geirfuglasker at one time rose to a greater height above sea-level, and so may have been a more suitable breeding-place for gannets.

On 27 April 1858 Newton(**248*a***) passed within two miles of Eldey and saw a great quantity of gannets about. He spent two months at Kirkjuvogur trying to get out to the Bird Skerries, but was prevented from doing so by bad weather.

A gannet's egg taken on Eldey on 7 June 1879 reached Wolley's collection originally from E. Lehn Schiöler(**173**).

In 1894(**306**) the Icelander Hjalti Jónsson climbed Eldey with four other men, and later told P. Nielsen, of Eyrarbakki, south Iceland, that he thought there were about 10,000 breeding pairs on the rock. Later E. Lehn Schiöler, the Danish ornithologist, asked Nielsen whether he was sure it was not 10,000 birds, to which Nielsen replied that he could not be sure(**173**). This was probably the first occasion on which men actually climbed to the top of Eldey (a gannet's egg, probably from this expedition, reached the Wolley collection through O. Ottoson in 1906), for the bird-fowlers who visited the rock previously to take the gare-fowl (*Alca impennis* L.) never climbed beyond the sloping ledge of rock below the main cliff. Gurney(**95**) records that in 1904 Jónsson told Nielsen that perhaps 6000 or 8000 birds would be enough. There is no doubt that this figure was far too low, as in years about 1908 the Westmann Islanders were taking about 4100 birds a year from Eldey. In 1919 Nielsen(**175**) said that about 10,000 breed there every year, but again could not say whether this referred to birds or pairs.

Slater(**204**) in 1901 and Hachisuka(**97**) in 1927 mention the colony but give no information about its size.

It is clear that there has been considerable confusion about the actual condition of the Eldey colony, and it was not until the publication of Roberts's researches (**190**) on the gannet colonies of Iceland that any accurate description of this colony appeared. Roberts quotes the account of his brother, who sailed round Eldey and estimated the population on the rock in 1934 at about 14,500 birds. Allowing 30 % for birds away fishing or flying over the rock, Roberts concludes that the breeding population was about 9000 pairs in 1934. Lockley & Salmon(**134**) have criticized Roberts's figure on the grounds that his basis of three acres covered by 9000 nests would involve a degree of crowding quite inconsistent with their experience of slightly under 5000 nests occupying 2 acres at Grassholm. This objection can now be answered from data obtained in 1939.

H. G. Vevers and L. S. V. Venables visited Eldey on 21 June 1939, with Gísli Gudmundsson, who had been to the top of Eldey a number of times in previous years with the bird-fowlers from Keflavík, south-west Iceland. Gudmundsson was able to climb on to the table-like top of the rock and to take a census of all the occupied nest-sites by direct counting. The number of breeding pairs on the cliffs, and on the sloping undercliff which forms the landing-place, were counted from the boat. There were very few non-breeding birds on the top of the rock—only between 50 and 100, and there were between 150 and 200 on the ledges near the landing-

place on the north-east side. The number of breeding pairs was as follows:

North-east	228	counted
East	182	,,
South: A	57	estimated
B	61	,,
C	100	,,
Flat top	8700	counted
Total	9328	

From rough measurements taken by Gudmundsson, it appears that the top, if assumed to be a flat but sloping surface, would have an area of about 9000 sq. m. (or 2·2 acres), and this would allow each nesting pair a little more than 1 sq. m. of space. But we know that the top is by no means flat, that it is thrown into two main ridges, as well as a number of smaller furrows, and that the whole space is occupied by gannets. Gudmundsson's measurements were taken with the help of a rope which he stretched in sections, so that only a few of the surface furrows would be taken into account in his measurements. The area of 2·2 acres would only hold, then, if the surface were almost completely flat; and the actual surface area available for nesting sites is considerbaly more than 2·2 acres and probably as much as, or more than, the 3 acres estimated by Roberts's brother (**190**). This revision of the population figure for Eldey, based on direct counts, confirms the previous estimate by Roberts; and at the same time it appears that the potential breeding area on the top of the rock is great enough to allow just under 9000 pairs to nest without danger of overcrowding.*

From accurate records kept by Séra Jes A. Gíslason of the Westmann Islands (and supplied to us by his son-in-law Thorsteinn Einarsson (**274**)) it appears that the average annual catch of gannets on Eldey in 21 years of the period 1910–39 was 3257. The total number taken in any one year varied from 200 to 4000. In 1939 Westmann Islanders killed 2000 young birds, of which only 1200 were removed on account of weather. It was estimated that about 2500 young birds were left alive.

Björnsson, in 1938 (**31**), advocated protection of the gannets on Eldey, and on 12 February 1940 the Icelandic Parliament (**111**) passed a law forbidding the capture of birds or collection of eggs on Eldey, thus making the rock Iceland's first bird sanctuary.

On 28 June 1941 an aircraft of Coastal Command (**300**) flew over Eldey and took photographs which, as far as we know, are the first ever taken of the top plateau of the rock. A grid estimate from one of these, which took in somewhat less than half of the top surface, gave *c.* 3916 nests, from which we can conclude that the number of breeding pairs on the top plateau was over 7832 and probably very much the same as in 1939.

On 21 February 1942 another Coastal Command aircraft took photographs of Eldey, which show that at that early date a large number of gannets were in occupation of sites on the top plateau and on the ledges on the cliffs.

On 22 July 1942 another aircraft took some excellent photographs, including a complete view of the top plateau, with good definition of the gannets thereon, except for a little dead ground at the east end. A grid estimate of the number of breeding pairs visible was 8440, from which we can again conclude that the number of breeding pairs, in all, was probably very much the same as in 1939.

Summary

Breeding between 1752 and 1764, 1821.

Great quantity about Eldey 1858; breeding 1879.

Possibly *c.* 10,000 breeding pairs 1894, 1904, 1919.

c. 4100 birds taken a year round 1908.

Mean annual catch 1910–39 3257, extremes 200–4000.

c. 9000 pairs 1934.

9328 pairs, 2000 young killed 1939.

Eldey declared a sanctuary, gannet-taking forbidden 1940.

1941 and 1942 population much the same as in 1939 (over 9000 pairs).

30. Grímsey

Grímsey is the most northerly breeding-place of the gannet, lying within the Arctic Circle. In 1786 Mohr (**152**) wrote that the gannet might sometimes be seen flying in the fjords in northern Iceland, but gives no breeding place in that area. The colony is first mentioned by Faber (**70**), who found three pairs on Grímsey itself, and ten or twelve pairs on a neighbouring stack, Hafsúlastapi, during a visit in 1819. In 1820 Faber (**72**) observed about twenty pairs in the whole colony, of which 14 pairs were nesting on Hafsúlastapi.

Newton (**171**) in 1863 and Slater (**204**) in 1901 record Grímsey as a breeding-place of the gannet, but have no first-hand information on the colony.

* It was computed (**13, 90**) that 20–25 million cormorants, gannets and penguins nest on Ichaboe Island, 26° S., 3 miles from the coast of Namaqualand, south-west Africa. This island is 1 mile long and 700 yd. wide, i.e. just over a million square metres in area. On the basis of the computation of numbers, and assuming the island to be flat (which is borne out by photographs), each pair would have a space only 20 by 40 cm., which is absurd.

We would suggest that, on the basis of its area and the fact that the birds are packed tightly over the whole of it, the island holds, at the most, two million pairs of birds. If they were all Cape Gannets (*Sula capensis* Licht.) we would suggest only one million.

Another example of computation by 'space' comes from Cato Island, in the South Pacific (**119**), where two million birds ('gannets', boobies, noddies and sooty terns) including 400,000 young were said to inhabit an area of 1/3 by 1/6 mile, i.e. 144,000 sq. m.—45 by 40 cm. per pair. This more nearly approaches possibility, since such a space might accommodate at least the smaller species.

Hantzsch (**99**) visited the island on 27 June 1903 (**173**) and found 50–70 pairs breeding on Hafsúlastapi and the cliff opposite. Roberts (**122**, **190**) found 21 occupied nests in 1933, all of which were on Grímsey itself. Hafsúlastapi collapsed some years before his visit and was abandoned by the gannets.

On 2 June 1934 an earthquake with its centre near Dalvík, northern Iceland, was felt on Grímsey, and a considerable amount of loose material was dislodged from the cliffs. On 6 July 1934 Holmes & Keith (**108**, **109**) descended to the colony and found only one occupied nest, although there were 41 non-breeding birds flying about; on the same ledge as the occupied nest they found about 10 unharmed but empty nests, and at the side of the ledge one dead gannet, and more nests, were partly covered with débris.

In July 1939 H. G. Vevers, L. S. V. Venables, F. C. Evans and W. G. Alexander visited the colony and counted 45 occupied nests. There were about 20 non-breeders in the vicinity (see also **232**).

In spite of the setbacks caused by the collapse of Hafsúlastapi and by the 1934 earthquake the Grímsey colony has remained in roughly the same place for at least 120 years. The 1939 count suggests that the colony is now in process of recovery, and future observations should provide valuable information on the changes in population of this typical small gannet colony.

Summary

13–15 pairs 1819; *c.* 20 pairs 1820.

50–70 pairs 1903; 21 pairs 1933; 1 occupied nest, over 10 empty nests (earthquake) 1934; 45 pairs 1939.

Supposed breeding in the Hólshreppur and Geithellna districts

In the statistical returns of the numbers of birds taken in the different counties of Iceland, there are a number of cases in which fairly large numbers of gannets appear to have been killed in districts other than those in which the three breeding colonies are situated. In 1921, 50 gannets were shown as captured in Hólshreppur, north-west Iceland (approx. position 66° 10′ N., 23° 16′ W.), and 30 were supposed to have been killed there in 1922 (**31**). Both Thorsteinn Einarsson (**274**) and one of the writers (**306**) have investigated these records, but there is no evidence that gannets have ever bred in this district.

In 1926 the same returns showed 1273 gannets as having been killed in Geithellnahreppur, a parish in south-east Iceland, which includes the island of Papey (64° 36′ N., 14° 11′ W.) (**31**). It was thought that most of these birds came from Papey, but in the summer of 1941 Thorsteinn Einarsson talked to Dr Ingolfur Gíslason who lives in Djúpivogur, and later visited Papey. Dr Ingolfur, and his father Gísli Thorvaldsson, the farmer on Papey, both told Einarsson that gannets had never bred or even attempted to breed on Papey.

There is, therefore, no evidence that gannets have bred in either of these two districts of Iceland, and it is possible that the returns given in the annual statistical summary of Iceland ('Fiskiskýrslur og hlunninda', a yearly part of *Hagskýrslur Islands* = *Statistique de l'Islande*, published in Reykjavík) have arisen either through a mistake in identification, which is unlikely, or a mistake in the statistical tables, the figures for kittiwakes caught having been put in the column reserved for gannets. The latter appears to be the most likely explanation.

It might be mentioned here that in 1901 Slater (**204**) mentions possible colonies off the north-west peninsula of Iceland, on or near Cape Reykjanes (as distinct from Eldey), and in Skagafjord. Likewise Newton (**170–173**) implies, in some of his remarks, that there may be breeding-places other than the three which we have described. There is no evidence for the existence of any such places.

(*h*) ST LAWRENCE GROUP

31. Gannet Rock, Grand Manan, New Brunswick

Verrill and Brewer visited this rock in 1859 and found one or two pairs of gannets nesting (**95**). They were told that there had been more before the lighthouse was built (Townsend (**228**) points out that the light was first shown in 1831). Bryant (**41**) visited the area in 1856, but does not appear to have visited Gannet Rock and makes no mention of gannets breeding there.

Boardman (**32**), in a list of local birds (1859), records that a few were breeding about the time he was writing; but it is not clear whether this information is based on his own observations or on Verrill's. It is probable that the gannets had been exterminated before 1870, and Herrick (**104**), who visited Gannet Rock in 1871 and 1872 found none breeding. Langille (**123**), writing in 1884, still listed this as a colony, but there is no evidence that he ever visited the neighbourhood.

Summary

Possibly fair numbers breeding before 1831.

1 or 2 pairs 1859.

Probably extinct before 1870; certainly so 1871, 1872 and since.

32. Gannet Rock, Yarmouth, Nova Scotia

Bryant (**41**) visited this gannet rock in June and July 1856 and found some hundreds of gannets covering the north end of the summit. He counted 150 nests, but there were no eggs, as the colony had been recently robbed by local fishermen. Birds in immature plumage were present in the ratio of one to every three in adult plumage.

Langille (**123**), who was in Nova Scotia in 1883, and Stearns & Coues (**211**), writing in this year, mention a colony on this rock. Langille stated that the gannet 'still breeds in considerable numbers', though we have no evidence that he visited the rock personally. It seems most probable that the last gannets were exterminated quite soon after Bryant's visit.

Summary

150 nests, all robbed, 1856; probably extinct soon afterwards, though possibly present until after 1883.

33. Bird Rocks, Magdalen Islands, Quebec

The gannet colony on the Bird Rocks, Gulf of St Lawrence, is first mentioned in Hakluyt's account of Jacques Cartier's voyage to Canada in 1534 (**95**). In Cartier's time there were three islands in the group, and he says 'these ilands were as full of birds as any medow is of grasse, which there do make their nestes; and in the greatest of them there was a great and infinite number of those that we call margaulx, that are white and bigger than any geese'. There can be no doubt that this account refers to the gannet.

Hore (**98**) visited Great Bird Rock in 1536, and he also 'found it full of great foules white and gray, as big as geese...'. As a further proof that these were gannets, he adds, 'the foules they flead and their skinnes were very like hony combes full of holes being flead off'.

In 1597 Charles Leigh (**98**) passed the islands and noticed the large number of birds. In 1626 Samuel de Champlain (**162**) saw the Bird Rocks, and said that they harboured incredible numbers of 'tangueux', a bird 'as large as a goose, with a very dangerous beak, and all white except the end of the wings'. At some time between these early records and 1860, when Bryant visited the colony, one of the rocks disappeared, by erosion of the soft sandstone.

Audubon (**22, 23, 24, 129**) visited Great Bird Rock on 14 June 1833. He could not land, and his description of the plateau on top of the Great Bird Rock is taken from his experienced pilot, Godwin. At the time of his visit the top of this rock was a quarter of a mile from north to south, and somewhat narrower from east to west. According to Godwin 'the whole surface of the upper platform is closely covered with nests, placed about two feet asunder, and in such regular order that a person may see between the lines, which run north and south, as if looking along the furrows of a deeply ploughed field'. Audubon learned from Godwin that the Labrador fishermen annually visited the Bird Rocks to get flesh to bait their cod-fish hooks. Godwin himself had visited the rocks, with the fishermen, for 10 seasons in succession, for this purpose; and on one occasion 'six men had destroyed five hundred and forty gannets in about an hour, after which the party rested a while, and until most of the living birds had left their immediate neighbourhood, for all around them, beyond the distance of about a hundred yards, thousands of gannets were yet sitting on their nests, and the air was filled with multitudes of others'. Enough were taken to supply bait for 40 boats. Audubon does not mention the Little, or North Bird Rock.

Dr Henry Bryant (**42**) visited the Bird Rocks in June 1860, and gave a good account of the gannets. He found that the group then consisted of the Great Bird Rock, and the Little, or North Bird Rock. He estimated that there were about 50,000 nests on the summit of Great Bird Rock, and that they were all on the northern half of the plateau. In addition, he considered that about 25,000 pairs in all were breeding on the sides of Great Bird Rock, and on the top and sides of Little Bird Rock. It is clear that there had been a considerable decrease since Audubon's visit, and this may be put down to the large numbers killed by fishermen.

Bryant's estimate of the numbers on *half* the Great Bird Rock plateau enables us to make a tentative estimate of the numbers present in Audubon's day (1833). Audubon's pilot showed him that the *whole* upper surface of the Great Bird Rock was closely covered with nests. Allowing for the erosion that may have taken place between 1833 and 1860, we can thus suggest that the population here may have been, in 1833, at least twice what it was in 1860, that is, *c.* 100,000 pairs; and that there may well have been as many pairs, then, in the other parts of the colony, as in 1860; that is, 25,000.

Further, the area of the Great Bird Rock plateau in 1833 was a quarter of a mile by somewhat less than a quarter of a mile—let us say two-thirds of a quarter-mile; that is, about 10·8 hectares. Godwin told Audubon that the gannets on this plateau were packed 'about two feet asunder'. Job (**113**), in 1900, and Bent (**28**), in 1904, found the close-packed nests on the top of North Bird Rock about 3 ft. apart. Our own study of Eldey, where gannets are packed on a flat plateau at their closest, shows that under such circumstances a little more than a square metre best represents the minimum space occupied by a nest (p. 200). We thus have further justification for putting the 1833 population of the top of the Great Bird Rock in the neighbourhood of 100,000 pairs; and we are putting the total population of the colony, in that year, between 100,000 and 125,000 pairs. Bird Rocks held by far the greatest gannet colony in the world in Audubon's and Bryant's days.

In 1864 Packard (**180**) visited the colony, and found two-fifths of the upper surface of Great Bird Rock covered with gannets' nests. Compared with Bryant's figure for half the upper surface, four years previously, this points to a population on the plateau of 40,000 pairs; we know that, at least up to Brewster's (**36**) visit in 1881, the population of the rest of the colony probably remained at its 1860 strength

(*c.* 25,000 pairs) and so place the 1864 numbers at *c.* 65,000 pairs.

In 1869 (**47**) a lighthouse was built on the Great Bird Rock plateau, and in 1872 Maynard (**149**) estimated the number of birds on the whole summit to be only 5000, i.e. 2500 pairs. We can thus provisionally place the total population in that year at *c.* 27,500 pairs, using the previous assumption about the rest of the colony.

In 1878 Cory (**53**) visited the rocks, found 'thousands' of gannets perched 'upon every conceivable projection' of Little Bird Rock. Gannets were also breeding on Great Bird Rock; he states that they were 'sitting upon the ledges in long rows', but does not mention whether they were on the top plateau. Great Bird Rock was then 102 ft. high, with about 4 acres of ground (1·6 hectares, three-twentieths of its surface area in 1833) on the summit. The Government had by now forbidden egg taking.

Brewster (**36**) visited the colony in 1881 and reported that the top of Great Bird Rock had been nearly abandoned; he found only about 50 nests there which had been recently robbed. The ledges on the sides of Great Bird Rock were still full, and the Little Bird Rock was probably full to capacity. He estimated that there were about 50,000 breeding birds in all, which agrees very closely with Bryant's estimate of 25,000 pairs on the Little Bird Rock and the sides of Great Bird Rock. Brewster also records that gannet flesh was still being used as bait by fishermen, who were also eating the eggs; and he condemns the negligence of the Canadian Government in allowing this to take place. He states that a few gannets were said to have bred on Shag Rock, near Grindstone Island. In the absence of further confirmation we have excluded this from the list of colonies.

Lucas (**139**) visited the colony on 9 July 1887 and found that no young were being raised on Little (North) Bird Rock, although there were about 150 pairs nesting on the pillar rock near it. This is the first evidence we have of Little Bird Rock being eroded into two parts. Lucas gives no details of the numbers or distribution of pairs on Great Bird Rock, but adds that M. Turbid estimated that there were about 10,000 birds in the whole colony.

Chapman (**47**), who landed on Great Bird Rock on 24 July 1898, found no nests on the summit plateau and suggests a total of 1500 birds, or about 600–750 breeding pairs for the whole rock. He was prevented by fog from visiting Little Bird Rock. He records that Great Bird Rock was then 350 yd. long, from 50 to 140 yd. wide, and rising from 80 to 140 ft. above sea-level. Its top area may thus have been about the same as in 1878. No more birds were now being taken for bait.

In 1900 (**113**) H. K. Job found the top of Great Bird Rock no longer occupied; but photographs show *c.* 450 occupied nests on its north-east and north-west corners, while there may have been more in dead ground. Little Bird Rock, now eroded into three stacks (**112**), had gannets' nests 'about a yard apart' all over the top of the 40 ft. high main block which (**114**) was divided into two sections. This block was said to be an acre in extent. (Thus, if it had been packed with nests this area would have held about 4000 pairs which, at the probable state of the colony in this year, is very unlikely.) On the detached pinnacle, or pillar, 60–70 ft. high, 40 nests are visible in a photograph. On 23 June many nests were empty on the main Little Bird Rock, and men from a schooner were seen to shoot 'quite a pile' of birds on the nest and take 'a couple of pails of eggs'.

In 1904 Bent (**28**) and Job (**114**) visited the colony. Bent records that less than 3000 birds were present, from which we may conclude that there were not more than 1500 nests in all, and probably less. Little Bird Rock consisted of two flat-topped parts, joined by a rocky beach, with perpendicular sides, and the pinnacle separated from them by water. On one of the main blocks the nests were about 3 ft. apart, according to Bent; and according to Job both sections of the main part were still covered with nests. Nobody had landed this year to rob them, either on Little or Great Bird Rocks. The keeper of the light had 'orders from the British Government to prevent all depredations upon the birds'.

In 1919 the Bird Rocks were made a Federal Bird Sanctuary by the Canadian Government (**64**).

Wynne-Edwards (**64**) published an estimate made in 1932 by F. L. Prest of Grosse Isle, who considered that there were about 700 birds on Great Bird Rock, and 300 on Little Bird Rock. The latter rock was being rapidly eroded and 'he did not think that it would remain above water at all for more than eight or ten years subsequent to 1933'.

In 1934 Gross (**92**) passed the rocks and estimated that there were about 2500 birds there in all.

It has so far proved impossible to obtain any count or estimate of the number of pairs at present breeding on the Bird Rocks, but it is probable that there are not more than 1000–1500 nests on both rocks together.

Summary

See Table 3, p. 204.

34. Bonaventure Island, Gaspé, Quebec

Bryant (**42, 43**) stated (*c.* 1860) that gannets bred on Percé Rock, near Cape Gaspé. This was certainly an error for Bonaventure Island, and the first evidence we have of the existence of a colony in this area; it was certainly a large one when Brewster (**36**) wrote in 1883.

Lucas (**140**) visited the colony in 1887 and thought there might be about 1500 pairs (3000 birds) breeding. Gurney (**95**) puts the colony at 3500 pairs, on the basis of an estimate made by Chapman, who visited Bonaventure in July 1898. Taverner (**221**)

estimated that there were about 4000 pairs of gannets in 1914 and 1915. The island was made a Federal Bird Sanctuary in 1918, according to Townsend (**227**), who visited Bonaventure on 10 and 18 July and 3 August 1919; he confirmed Taverner's estimate.

Duval (**63**) writes: 'In 1923 there were forty-seven nests of gannets on a ledge in the sanctuary that I had not seen occupied by gannets before. In 1924, there were seventy-two. This year [1925]... there are about four hundred occupying that ledge.' Bond (**33**) also records that in 1925 the gannets were apparently increasing.

and considered that *c.* 6000 pairs were nesting in May, 1939. Mr Grinnell (**280**) visited the colony on 28 and 29 July 1939 and estimated that there were 9000 adult gannets on the ledges. By doubling this figure he arrived at a total of 18,000 adults (to include those flying and swimming) but his original figure of 9000 birds on the ledges probably included a number of birds present at their nests together with their mates. If, as elsewhere, we regard these birds as 20 % of the whole, we arrive at a figure of 7200 nests.

In May 1940 the colony was again visited by Dr Lewis, who estimated that at least 16,000 adult gannets were present (**291**). From subsequent observations at Anticosti on the number of gannets present on a cliff at any one time, and the relation of this number to a direct count of nests, Dr Lewis would prefer to put the total number of adults in 1940 at 13,360, giving a breeding population of *c.* 6680. On the basis of these valuable observations we now regard the breeding population in 1939 as 6600–7000 pairs, rather than 7200 pairs as previously reported (**78**).

In May 1940, a photograph (**18**) showed that the birds had now invaded the flat ground at the tops of the cliffs, and were nesting near pine trees.

Table 3. *The history of the Bird Rocks colony (all figures refer to the number of pairs)*

Year	Great Bird Rock	Little Bird Rock	Approx. total no.	Remarks	References
1534	Breeding	Breeding	Very many	Probably a third rock	(**95**)
1536	,,	,,	,,	,, ,,	(**98**)
1597	,,	,,	,,	,, ,,	(**98**)
1626	,,	,,	,,	,, ,,	(**162**)
1833	Whole upper surface covered, *c.* 11 hectares	—	*c.* 100,000–125,000	Much slaughter *c.* 1823–32 for bait	(**22**), (**23**), (**24**), (**129**)
1860	Half upper surface covered, *c.* 50,000 on plateau	*c.* 25,000 here and on sides of Great Bird Rock	*c.* 75,000	—	(**42**)
1864	Two-fifths upper surface covered, *c.* 40,000 on plateau	—	*c.* 65,000	—	(**180**)
1869	Lighthouse built	—	—	—	(**47**)
1872	*c.* 2500 on plateau	—	*c.* 27,500	—	(**149**)
1878	Now eroded to *c.* 3/20 of 1833 top area, estimated 1·6 hectares; breeding on sides	'Thousands' breeding	—	Egg taking forbidden by Government	(**53**)
1881	50 on upper plateau	Full to capacity	*c.* 25,000	Bird and egg taking still continues	(**36**)
1887	—	Eroded into two parts; no young raised main part, 150 pairs on pillar	*c.* 5,000	—	(**139**)
1898	None on upper surface, 650–700 on sides	Not seen	—	Birds not taken	(**47**)
1900	At least 450 on sides	Eroded into three pieces; over 40 on pillar; said to be fully occupied	—	Birds and eggs taken	(**112**), (**113**)
1904	—	In three pieces; said to be fully occupied	*c.* 1,500	No birds or eggs taken	(**28**), (**114**)
1919	—	—	—	Federal Bird Sanctuary created	(**64**)
1932	*c.* 350	*c.* 150; rock being rapidly eroded	*c.* 500	—	(**64**)
1934	—	—	*c.* 1,250	—	(**92**)

In 1932 Dr Harrison F. Lewis estimated the breeding population at 6000 pairs (**64**). On the basis of this and other estimates by Dr Lewis, Wynne-Edwards *et al.* (**65**) estimated that there were *c.* 6500 pairs in 1934. Wynne-Edwards (**273**) visited the colony in August 1938 and estimated the population at 7000 pairs.

For the 1939 census we have received reports from Mr William Duval, Honorary Warden of the Bonaventure Federal Bird Sanctuary, and from Mr Lawrence I. Grinnell of Ithaca, N.Y. Mr Duval (**271**) estimated a total of 14,000 birds in the colony,

 R.A.F. official photo

Photo. 14. Eldey, Iceland, 22 July 1942, approximately from the north. Height *c.* 400 ft. A grid estimate from this photograph, which is the first ever published (as far as we know) of the top of Eldey, shows that *c.* 8400 pairs were breeding on the plateau. In 1939 the population of the entire rock was *c.* 9300, and of the top plateau *c.* 8700. Reproduced by permission of Coastal Command, Royal Air Force.

 H. G. Vevers

Photo. 15. Gannet with newly hatched young on Brandur, Westmann Isles, Iceland, 2 July 1939.

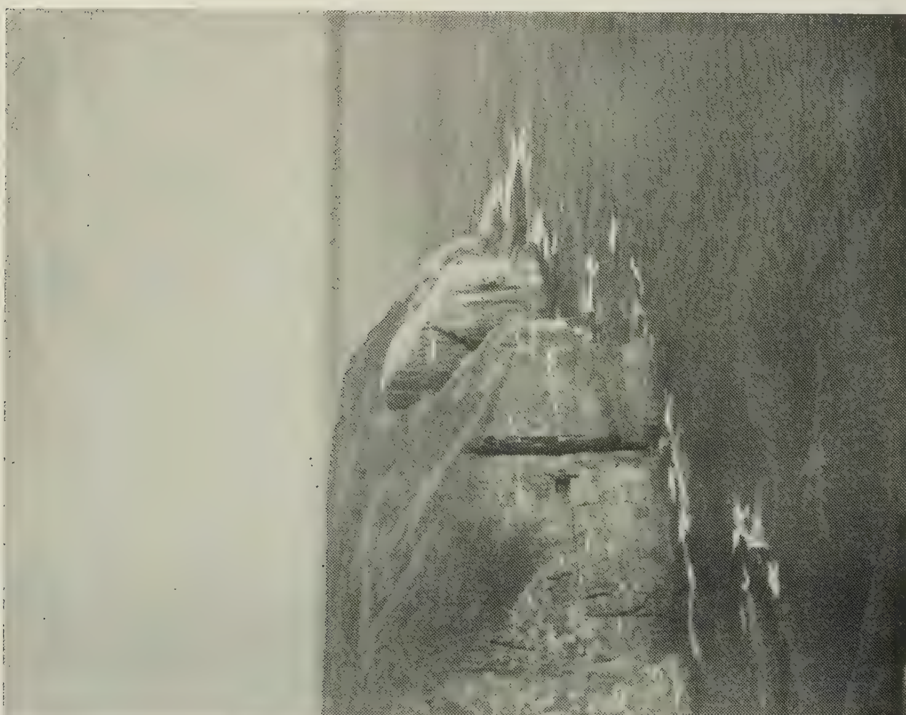


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Photo. 16. General view of the gannet colony at Cape St Mary, Avalon Peninsula, Newfoundland, 11 July 1939, approximately from the west. Height of gannet stack *c.* 290 ft. *c.* 4300 pairs were nesting in this year.

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Photo. 17. Upper half of the gannet stack, Cape St Mary, 11 July 1939, approximately from the north-west.

Summary

Colony present *c.* 1860.

Large colony 1883; *c.* 1500 pairs 1887.

c. 3500 pairs 1898.

c. 4000 pairs 1914, 1915; protected 1918; *c.* 4000 pairs 1919.

Increasing 1923, 1924, 1925.

c. 6000 pairs 1932; *c.* 6500 pairs 1934; *c.* 7000 pairs 1938; 6600–7000 pairs 1939; *c.* 6680 pairs 1940.

35. Perroquet Islands, Mingans, Quebec

The Perroquet Islands are the most westerly of the Mingan group, lying off the north shore of the Gulf of St Lawrence. Gannets at one time bred on the north-western island of the Perroquets, now occupied by a lighthouse.

Comeau (**51**) mentions 'two immense colonies of gannets and puffins' on the Perroquets in the years 1857–9, but does not give any details of their situation. Coues (**54**) passed close by the island in 1861 or before, and referred to it as a great breeding place of the gannet. Brewster (**36**) actually landed there in 1881, but found only empty nests and occasional broken eggs, as the colony had been raided the day before by Indians. When he passed the island a week before this visit he saw hundreds of gannets nesting. Frazar (**80**) visited the Mingan group in 1884 and mentions a small colony of gannets although he evidently did not visit the actual rock. Lucas (**139**) was there on 11 August 1887 and saw a few gannets, none of which was breeding.

Bent (**28**) visited the Perroquets with Townsend in June 1909, but saw no gannets breeding and was told that they had been driven away by persecution. Townsend (**226**) passed the islands again in July and August 1912 and saw five birds in the latter month. He was told that a few gannets came every year, but that none had bred there for a long time.

Lewis (**127**) also observed gannets flying near the Perroquet Islands in about 1922, but points out that there is no hope of their ever breeding on the same rock again, as long as the lighthouse is there.

Summary

'Two immense colonies' 1857–9; great breeding-place *c.* 1861.

Eggs and nests destroyed, but still hundreds attempting to breed 1881; small colony 1884; a few present, none breeding 1887.

None breeding 1909, 1912, *c.* 1922.

36. Gull-cliff Bay, Anticosti Island, Quebec

Verrill (**233**) wrote that gannets were quite common in the vicinity of Anticosti Island in the summer of 1861, but none were found breeding there.

Capt. O. Mercier hinted to Lewis (**128**) that gannets may have been present at the cliffs of Gull-cliff Bay since 1913. Brooks (**37**) stated that M. Gagnon had told him that a colony had bred, presumably in the summer of 1919 or 1920, on the cliff near Wreck Point, Anticosti. Dionne (**59**), in 1920, merely listed the gannet as very common off the coasts of the island.

Anderson (**4**) was the first to publish a mention of 'a number' of gannets nesting at the eastern extreme of Gull-cliff Bay, Anticosti, before 1922. Lewis (**128**) himself visited the colony in June 1922 and found gannets numerous near West Point. In 1923 Johansen (**128**) found 'a score or so of gannets' nesting on the south-east side of Table Head, and also mentioned 'hundreds' of gannets nesting further east at Gull-cliff Bay, the majority being on the high cliffs near Cape Sandtop. It would appear from Johansen's notes that there were two more or less distinct breeding colonies.

Taverner (**222**) visited Anticosti in 1928, and later wrote: 'Table Head and Sand Point have been given as sites of gannetries. Both of these points along the coast we travelled but saw no evidence of gannets breeding on them, and it was not until we reached Gull Bay that any nesting birds were seen. At Gull Bay we found about 500 nests scattered among those of the kittiwake.' Wynne-Edwards (**64**) mentioned the colony and with Lockley & Salmon (**65**) quoted Taverner's estimate of 500 pairs with nests in 1928.

Dr Harrison Lewis (**291**) visited the colony again in 1940 and we are indebted to him for the following information: The gannets were only found nesting at Gull-cliff Bay and were occupying ledges on a limestone cliff over a total extent of three miles. The cliff is about 116 ft. high and the ledges are narrow and mostly short. A count of nests showed that 496 were occupied by breeding pairs. Dr Lewis considers it unlikely that there will be any great increase in this colony since all the suitable ledges are already occupied by gannets or European cormorants. He also observed a tendency for the colony to spread by nesting on top of the cliffs, but this is evidently rendered difficult by white-tailed deer which crop the grass right to the edge of the cliff and by foxes which probably kill a certain number of the birds not actually on the cliff face. In support of this he found the mangled remains of some gannets a little back from the cliff top.

Summary

Not breeding 1861.

Possibly present since 1913.

Breeding in some numbers 1919 or 1920, 1921, 1922.

Possibly more than 100 pairs 1923; *c.* 500 pairs 1928.

496 occupied nests 1940.

37. Cape St Mary, Avalon, Newfoundland

The history of this colony is now known in some detail, thanks to the visits of V. C. Wynne-Edwards (**64**) in 1934, and O. H. J. Davies and R. D. Keynes (**268, 289**) in July 1939, and their conversations with local inhabitants such as Daniel Young, of St Bride's, A. Conway, the present lighthouse-keeper and his father J. Conway, who was keeper before him.

In about 1877, Daniel Young told Wynne-Edwards, there were no gannets at all. J. Conway told Davies that in the year when, as a young man, he went to sea, there were nesting gannets, but not more than 3 pairs. He could prove that this year was 1879. Daniel Young used the same method, of recollecting the year in which, as a young man, he went to sea, when he informed Wynne-Edwards that there were no more than 8 or 10 pairs in about 1883. In 1889 J. C. Cahoon succeeded in climbing the rock (**30**, **64**); he was a professional collector forbidden to divulge information, and to this day we know nothing of what he probably knew (before he was killed in 1891) about the early history of this colony.

In 1890 H. L. Bigelow (**30**) found the rock on which the gannets nest, about 290 ft. high and separated from the mainland, 'bearing on its summit a plateau about an acre in extent, which is literally covered with birds, for the Gannets and Murres were so thick that not a foot of rock could be seen, for what was not birds was eggs'.

James Conway told Davies that in 1913 the rock was half-covered with breeding gannets. This may mean that the population was of the order of 2000 pairs, for when Wynne-Edwards paid his visit in 1934, and found *c.* 4000 pairs, he records that the nests covered the whole of the outer fan-like slope of the summit and the upper part of the cliff below it.

In 1918 English (**67**) visited the colony, but merely stated that 'thousands' were present.

In 1934 A. Conway told Wynne-Edwards that the gannets 'have increased by one-quarter in the last ten years'. Based on this remark, the population in 1924 would appear to have been about 3200 pairs. Arthur Conway also told Davies that the gannets spread from the stack to the mainland opposite in about 1926 (one area) and 1929 (another), but only used it as a resting-place until 1931, when they first attempted to breed on the mainland.

Wynne-Edwards visited the colony on 23 June 1934. There were few nests on the upper part of the summit plateau which was used as a standing-ground. His photographs showed that there were from 500 to 700 birds in adult plumage standing on the mainland slope opposite. From 1931 to 1934, A. Conway told him, as many as a dozen nests had been built on the mainland east of the rock, but they never survived the first visit of the fishermen who, while they fish off the Cape for four weeks in June and July, kill (A. Conway told Davies) about 400 birds a year in spite of the Federal Game Laws.

Wynne-Edwards estimated the population as 4000 breeding pairs. He counted 5000 individuals, at one time, on the rock; but both he, and Davies and Keynes, from their several experiences at the colony, agree that, allowing for those nests at which both members of the pair were present, the number of occupied nests was *c.* 4000. Wynne-Edwards did not believe that there were more than 4500 nests; and we accept the figure of 4000.

In 1938 there were 18 nests on the mainland to the east of the rock, and 7 or 8 on a neighbouring mainland area, according to A. Conway. Eggs on the mainland are invariably smashed by the fishermen and in 1939 only two or three were found here.

Davies and Keynes's (**58**) figure of 4294 ± 350 pairs was based on counts and estimates of the numbers of birds present on the rock in 1939. It was divided into nine groups and independently observed by both ornithologists. The mean counts of each group were added to make the total which includes an allowance of 50 nests not seen. The percentage which was estimated rather than counted direct was 13·8. Counts of sample groups showed that 15 % of nests were occupied (at the time of counting) by both birds—this figure was used to correct the total.

Summary

Not breeding *c.* 1877; 3 pairs 1879.

8–10 pairs 1883.

Gannets 'thick' 1890.

c. 2000 pairs 1913; 'thousands' 1918.

c. 3200 pairs 1924.

Gannets used one mainland area as resting-place 1926, two such areas 1929; first attempted to breed on mainland 1931; up to 12 nests on mainland 1931–4; but nests interfered with by fishermen.

c. 4000 breeding pairs 1934.

25–26 nests mainland 1938, 2–3 1939, eggs smashed by fishermen.

c. 4294 nests 1939, fishermen taking about 400 adults annually.

38. Bacalieu Island, Newfoundland

H. S. Peters (**184***a*) found a gannet colony 'of approximately two hundred nests' on the cliff on the east side of Bacalieu Island, on 24 June 1941. This is a rocky island several miles from the small fishing village, Bay de Verde, out to sea off the northernmost tip of the Avalon Peninsula, and in the mouth of Conception Bay. Peters writes: 'Old residents told me that the gannets have been there for about forty years, but the colony has not been before recorded.'

Summary

Possibly breeding since *c.* 1901.

c. 200 pairs 1941.

39. Funk Island, Newfoundland

Jacques Cartier found gannets breeding on Funk Island in 1534 (**82**), after which there is a long period in which we have no records from this island. Local fishermen told Lucas (**139**) that gannets were breeding there in about 1857, but there were certainly none there at the time of Milne's visit on 20 July 1873, or Lucas's on 22 July 1887 (**140**).

Bent (**28**) writes in 1922 that gannets 'are said to have nested on Funk Island many years ago, but

after the extermination of the Great Auk, the gannets probably shared a similar fate'

Wynne-Edwards (**64**) sailed round the island in 1934 and is quite certain that no gannets were nesting there at that time. Gilliard (**82**) visited Funk Island in June 1936 and found a total population of about 40 gannets, of which 7 pairs were breeding, the remainder being non-breeders.

It has not been possible to obtain further information on this colony; Davies & Keynes (**268**, **289**) made a valiant, but unsuccessful attempt to get there in 1939.

Summary

Breeding 1534.
Breeding not proved 1857.
Not breeding 1873, 1887, 1934.
7 pairs breeding 1936.

Other places in Newfoundland—Labrador—Quebec

In 1838 Audubon (**22**) writes: 'George C. Shattuck, M.D. of Boston, while with me at Labrador, caught one [gannet] which he found walking amongst a great number of guillemots, on a low and rocky island.' Lewis (**129**) shows that Audubon travelled along the north shore of the Gulf of St Lawrence between Natashquan and Bradore Bay in 1833. This is entirely in the modern province of Quebec, and was the extent of Audubon's 'Labrador' experience. 'Labrador', as a term in use in Audubon's day, included the country on the north shore of the Gulf of St Lawrence.

Audubon also states: 'The period of their arrival at their *breeding-grounds* [our italics] appears to depend much on the latitude of the place; for, on the Bass Rock, . . . the gannets are first seen in February, whereas in the Gulf of St Lawrence they rarely reach the Great Rock until the middle of April or beginning of May; and at Chateau Beau in the Straits of Belle Isle, not until a fortnight or three weeks later.' Chateau Beau can be identified with Chateau Bay, 51° 58′ N., 55° 55′ W. There is no evidence that Audubon ever got there himself (it is just in modern Labrador), or why he should have hinted that it was a breeding-ground.

In 1913 Gurney (**95**) writes: '*The Gannet Islands, Labrador.* Some 400 miles north of Funk Island, and about ten from the mainland of Labrador, are three islands named the Gannet Islands and Gannet Rock [53° 56′ N., 56° 35′ W.]—an appellation which may possibly signify that Gannets once bred there, but the names may have an entirely different origin. Professor Newton has pointed out that these islands are several times mentioned in a journal by George Cartwright [1792], but no hint is given of Gannets breeding upon them. Mr W. Grenfell, who has often passed them, tells me that they reach to about 200 feet at the highest point.'

In 1934 Wynne-Edwards (**64**) made 'a coastal trip in the Government steam-trawler "Cape Agulhas" from St John's to Gready Island, Labrador (53° 50′ N.), and back through the Straits of Belle Isle to Corner Brook. We passed [he writes] and visited many islands off the outer coasts of Newfoundland and Labrador, including Funk Island. I had half expected to come across a small gannetry on this coast, in view of the oft-observed presence of Gannets in the neighbourhood of Belle Isle. I am, however, satisfied that no such colony exists, since I have now seen at close quarters every suitable island within 100 miles of this place, having made a special point of doing so.'

We know that since Wynne-Edwards's journeys the Funk Island station has been recolonized, and the Bacalieu Island colony discovered. We cannot entirely rule out the possibility of there being, yet, unknown colonies of the gannet on the lonely coasts of Quebec, Newfoundland, or even Labrador.

3. SUMMARY

1. In 1939 an attempt to make a census, within the space of one breeding season, of the world population of the gannet (*Sula bassana* L.), was organized by the writers.

2. In 1939 gannets were breeding at 22 colonies. Three of these were in south-west Britain, 2 in east Britain, 2 in west Britain, 6 in north Britain and the Faeroes, 3 in Iceland and 6 in the Gulf of St Lawrence. Of these, all the colonies in Britain, the Faeroes and Iceland were visited in 1939. Of the colonies in the Gulf of St Lawrence 2 were visited in 1939, 1 in 1940, 1 in 1941 (not having been discovered previously) and 2 for the last time in 1934 and 1936. The colonies not visited in 1939 contained about 2·5 % of the world population.

3. The history of the 39 places where gannets breed, have bred, have been suspected to have bred, or have occupied cliffs or ledges in the breeding season is fully discussed, as are the results of the 1939 census. A summary is provided in Table 4. All save 6 which are of doubtful or vague history are shown on Map 5.

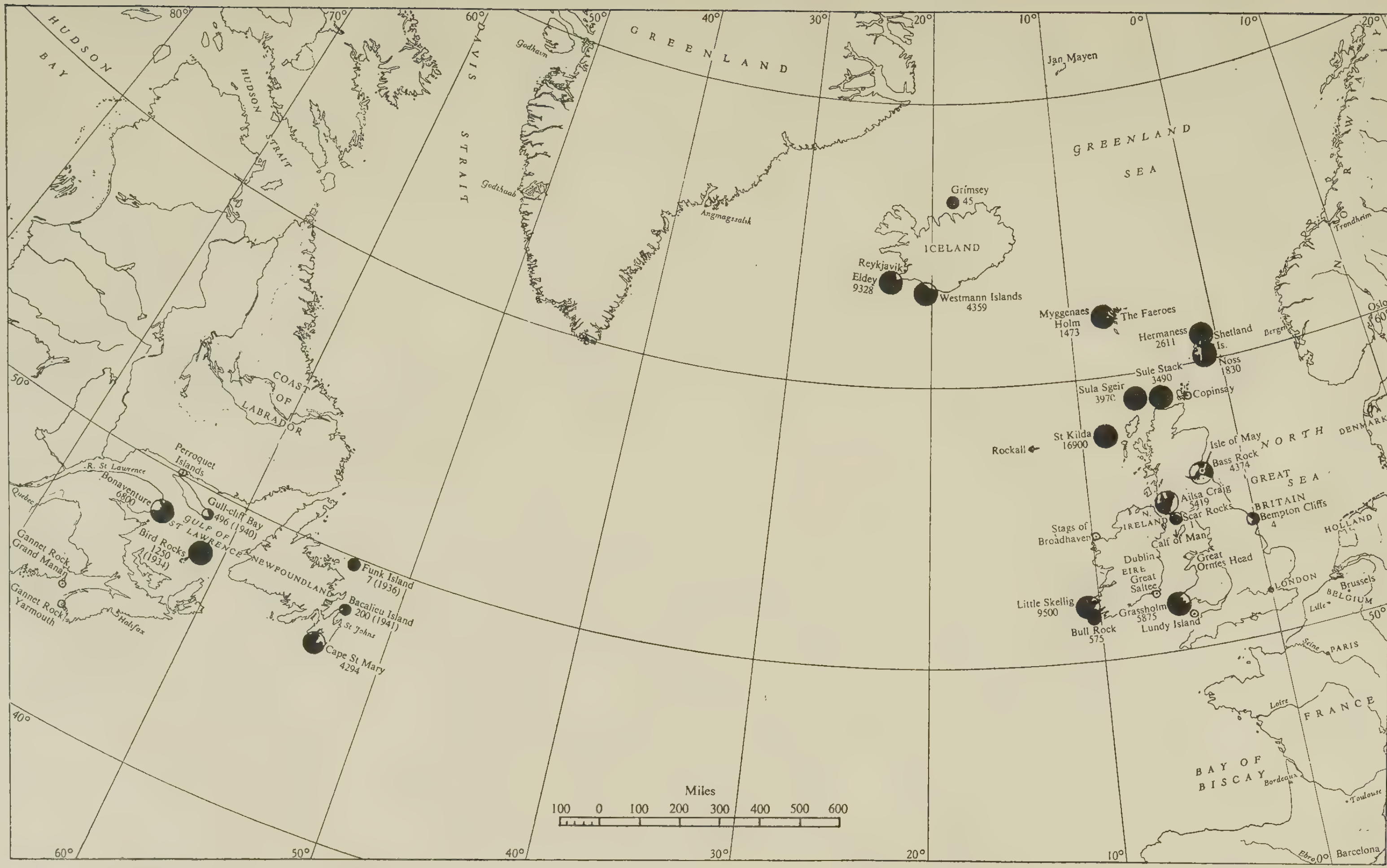
4. The number of breeding individuals of *Sula bassana* in 1939 was 165,600 ± 9500. The limits of error were worked out from a sample of over half the population, which was breeding at colonies where more than one observer took part in the census, and represent the maximum recorded discrepancy between the counts of the different observers of each group of nests in the colonies.

5. A full discussion of trends in the gannet's population during the last hundred years, and of certain ecological points and biological matters which arise from this survey, is reserved for Part 2 of this paper.

Table 4. *Summary of the history and present population of the world's gannet colonies (all figures refer to the number of pairs)*

Group	No.	Colony	Colonies of ancient history: First known breeding	Colonies of ancient history: Last known breeding	Colonies of ancient history: Birds last seen on station	Stations established or re-established as colonies, or occupied in the breeding-season, in recent times: Birds first seen on station	Stations established or re-established as colonies, or occupied in the breeding-season, in recent times: First known breeding	Stations established or re-established as colonies, or occupied in the breeding-season, in recent times: Birds last seen on station*	Present population: No. of breeding pairs	Present population: Year of census
South-west Britain	1	Gulland Rock	?1468	?1468	?1468	—	—	—	—	—
	2	Lundy Island	1274	1903	1907	1922	—	1922	—	—
	3	Grassholm	—	—	—	Between 1820 and 1860	Between 1820 and 1860	—	5,875	1939
	4	Great Orme's Head	—	—	—	1941	—	1941	—	—
	5	Little Skellig	1700	—	—	—	—	—	9,500	1939
	6	Bull Rock	—	—	—	1853	1856	—	575	1939
	7	Great Saltee	—	—	—	1929	1929	1943	0	1939
	8	Stags of Broadhaven	c. 1756	?1836	?1836	—	—	—	—	—
East Britain	9	Bempton Cliffs	—	—	—	1924	1937	—	4	1939
	10	Bass Rock	1447	—	—	—	—	—	4,374	1939
	11	Isle of May	Before 1850	Before 1850	Before 1850	1922	—	1922	—	—
West Britain	12	Calf of Man	?1586	?1652	?1652	1939	—	1939	—	—
	13	Scar Rocks	1883	1883	1883	1939	1939	—	1	1939
	14	Ailsa Craig	1526	—	—	—	—	—	5,419	1939
	15	Islay	?1703	?1703	?1703	—	—	—	—	—
	16	Eigg	?1549	?1549	?1549	—	—	—	—	—
	17	Rum	?1549	?1597	?1597	—	—	—	—	—
North Britain —Faeroes	18	Oigh-sgeir Eagach	19th cent.	19th cent.	19th cent.	—	—	—	—	—
	19	St Kilda	1684	—	—	—	—	—	16,900	1939
	20	Rockall	—	—	—	?1810	—	1941	—	—
	21	Sula Sgeir	1549	—	—	—	—	—	3,970	1939
	22	North Rona	Before 1883?	Before 1883?	Before 1883?	—	—	—	—	—
	23	Sule Stack	1710	—	—	—	—	—	3,490	1939
	24	Copinsay	—	—	—	1907 or 1908	—	1925 or 1926	—	—
	25	Noss	—	—	—	1911 or 1912	1914	—	1,830	1939
	26	Hermaness	—	—	—	1917	1917	—	2,611	1939
	27	Myggenaes Holm	1673	—	—	—	—	—	1,473	1939
Iceland	28	Westmann Islands	c. 1700	—	—	—	—	—	4,359	1939
	29	Eldey	Before 1764	—	—	—	—	—	9,328	1939
	30	Grímsey	1819	—	—	—	—	—	45	1939
St Lawrence	31	Gannet Rock, Grand Manan	Before 1831	1859	1859	—	—	—	—	—
	32	Gannet Rock, Yarmouth	1856	?1883	?1883	—	—	—	—	—
	33	Bird Rocks	1534	—	—	—	—	—	1,250	1934
	34	Bonaventure	c. 1860	—	—	—	—	—	6,800	1939
	35	Perroquet Islands	1857	1884	1887	—	—	—	—	—
	36	Gull-cliff Bay	—	—	—	?1913	?1913	—	496	1940
	37	Cape St Mary	—	—	—	1879	1879	—	4,294	1939
	38	Bacalieu Island	—	—	—	c. 1901	c. 1901	—	200	1941
	39	Funk Island	1534	1534	1534	1936	1936	—	7	1936
								Total	82,801 pairs 165,602 individuals	

* This column only specifies those stations where birds have been seen recently in the breeding season, but where colonies are not now *established*.



Map 5. The world distribution and breeding population of the gannet. Figures refer to the number of breeding pairs in 1939, unless otherwise indicated. ● colonies of over 1000 pairs. ● colonies of under 1000 pairs. ⊙ colonies now extinct. ← stations where gannets occupy cliffs or ledges in the breeding season, but have not bred. Six stations of doubtful or vague ancient history have been omitted. Based upon sketch for British Council Map No. 3, by the Royal Geographical Society, by permission.

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List of informants. Those in the following list have privately supplied information about gannet colonies. All of them have gone to considerable trouble, and many have suffered considerable expense, in replying to correspondence, acting on suggestions, and making journeys in the field. Two crossed the Atlantic, with the investigation of two colonies as one of their main objectives. Six persons made separate, special journeys in Ireland. Four observers spent three weeks in a small yacht, round the north coast of Scotland. Five men covered the colonies of Iceland, Faeroes and Shetland. We are very grateful to all of them. (The writers are included in the list for the purpose of reference.)

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RATTUS RATTUS ON LUNDY

By J. S. WATSON, *Bureau of Animal Population, Oxford University*

The history of the ship rat (*Rattus rattus*) on Lundy, an island off the Devonshire coast, is known in some detail and has been traced down to 1925, when it was described as 'though not entirely extinct it is but rarely met with', and it was alleged that the ship rat had been superseded by the brown rat (*R. norvegicus*) (Loyd, 1925). A few years previously, however, Coward (1907) obtained all three forms of the ship rat, and it seems unlikely that it ever was completely extinct on the island.

From time to time the population has undoubtedly been replenished by rats from ships wrecked on the island, in particular from a Greek ship driven ashore in 1928, and reported to have been badly infested.

Three *R. rattus frugivorus* were caught by me in the first fortnight of July 1942 on Lundy. All three were trapped under piles of driftwood, one in a cave near the harbour, the other two in the open on the shore below Rat Island. Breakback traps were used and baited with limpet.

All the rats were adults, two being males the other a female. The skulls of two which were preserved showed remarkable resemblance to that of *R. norvegicus*, the supra-orbital ridges being nearly parallel as in that species; but the skull in profile had the typical slightly domed roof of *R. rattus*. It has been suggested that this resemblance to *R. norvegicus* may be due to a strengthening of the skull resulting from the strenuous conditions of life on the shore. The specimens were kindly examined by Dr M. A. C. Hinton who pronounced them to be *R. rattus*. The specimens are deposited in the Bureau of Animal Population.

Unfortunately, it was impossible in the time available to estimate the numbers or distribution of the species on the island. *R. norvegicus* appears to be plentiful and widely distributed.

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Coward, T. A. (1907). 'Some notes on the mammals of Lundy.' Mem. Manchr. Lit. Phil. Soc. 52, no. 6: 1–14.

Loyd, L. R. W. (1925). 'Lundy: its history and natural history', p. 216. London.

Photo C. Elton

Photo. 1. Pasture country, with blue (evergreen) oaks, in the Upper Sonoran Zone, Sierra Nevada. Habitat of ground squirrels (*Citellus beecheyi*), kangaroo rats (*Dipodomys*), pocket gophers (*Thomomys*), Californian quail (*Lophortyx californica*), and rattlesnakes (*Crotalus viridis*). The quail roost in the oaks.

Photo C. Elton

Phot. 2. Ground squirrel (*Citellus beecheyi*) having a dust bath. Note pasture with cow dung; and turkey mullein (*Eremocarpus*). This species of squirrel carries plague in some other parts of California.

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(Acknowledgement is made to the Staff of the San Joaquin Experimental Station, for the opportunity of taking these photographs.)

THE JOURNAL OF ECOLOGY

(Vol. 31, Nos. 1, 2, May and November 1943)

No. 1 contains a valuable account (with a good map) of the tidal condition in the Bristol Channel by R. Bassindale. There is also a shorter study of the vegetation of Cornish sea cliffs by Ian Hepburn. A large part of the number consists of four contributions to the 'Biological Flora': *Juncus macer* and *J. filiformis* by P. W. Richards; and *Rhamnus cathartica* and *Frangula alnus* by H. Godwin. There is also a note on the taxonomic usages to be employed in this Flora. Critical and full reviews are given of Dr Rayner's work on the mycorrhizal relations of *Pinus*, and of Salisbury on the Reproductive Capacity of Plants.

No. 2 contains six original papers and a review of the *Journal of Animal Ecology*. One of the original papers is Dr H. Godwin's Presidential Address to the British Ecological Society in 1943, on the coastal peat beds of the British Isles and North Sea. From various examples and from the general point of view, consideration is given to the plant content of the peats, to their dating by means of pollen analysis and to their value as evidence of former sea-levels against the background of eustatic and isostatic factors in land and sea-level changes. In the vegetation of the Karamola District, Uganda, A. S. Thomas continues his work on East African vegetation with particular reference to the effects of grazing and of other cultural practices. S. P. Chu, in discussing the influence of the mineral composition of the medium on the growth of planktonic algae, deals especially with the effects of varied concentrations of inorganic nitrogen and phosphate phosphorus upon growth in pure culture. The relation of the culture results to field investigations is also indicated. Another algal subject is treated by H. M. David in a paper on the autecology of *Ascophyllum nodosum* with particular reference to its occurrence on the coast of Cardiganshire and its seasonal and growth cycles.

W. H. PEARSALL

A CALIFORNIAN COMMUNITY

C. B. Hutchison & E. I. Kotok (1942). *The San Joaquin Experimental Range.* University of California, College of Agriculture, Agricultural Experiment Station, Bull. No. 663: 1–145. University of California, Berkeley.

The following articles in this volume are more especially reviewed here:

E. E. Horn & H. S. Fitch: *Interrelations of rodents and other wild life on the range.*

T. I. Storer, F. P. Cronemiller, E. E. Horn & B. Glading: *Studies on valley quail.*

To the ecologist, California is a fascinating land, because it combines the most striking and beautiful natural life zones with extraordinary problems resulting from the advance of cultivation into wild country and the spread of introduced animals and plants. In spite of its more obvious cultivated crops, pasture is one of the great resources of California, there being some sixty million acres of it out of about a hundred million altogether. Several thousand feet up in the foot-hills of the Sierra Nevada, in granite rocky country covered with dry pastures and savannahs of evergreen oaks and digger pines, an experimental station was set up to study the agricultural aspects of pasture problems, and this led on to the study of rodents, game birds and other animals as well. By the courtesy of the research workers at this station I was able in 1938 to get photographs that give a good idea of the kind of habitats that were being studied, and two of these are given in Plate 11. There is still a rich wild animal community that includes, among other forms, many predatory birds and mammals, and a great number of rattlesnakes (*Crotalus viridis*), more than one per acre! Altogether about 80 land vertebrates are mentioned in this report.

The most important rodents are the ground squirrel (*Citellus beecheyi*), in some other parts of California a carrier of bubonic plague, and here the greatest rodent destroyer of forage; the pocket gopher (*Thomomys bottae*), a subterranean species belonging to a purely Nearctic family, is one of the most abundant forms, also a forage eater, but causing benefits by its winter burrowing activities; the kangaroo rat (*Dipodomys heermanni*), which is abundant but fluctuates strongly from year to year; and the cottontail rabbit (*Sylvilagus auduboni*), with a density of one per acre in 1939, an important competitor against grazing stock. The predator fauna of ten hawks and four owls makes the British naturalist shake his head in envy. No great detail is given in this report of the methods of census and marking adopted to determine densities, and one may presume that after the War is over these important details will be published. The subject was studied partly by means of enclosures containing different wild colonies of rodents, and the animal observations were matched by careful quadrat work by a botanist.

The scale of operations can be realized from the calm statement that 'in the 1938 and 1939 seasons, and to June 30, 1940, a total of 515 rattlesnakes were caught alive on the Range, marked, and released after measurements, weight, and other data had been recorded for each. Subsequently, many of the marked snakes were again found and were caught or killed.... For the entire area of 4700 acres a population of 5000 rattlesnakes seems conservative.' One certainly would prefer to be conservative! It was estimated that rattlesnakes fed predominantly on the ground squirrels, and that they were an important agent also in causing nesting losses of valley quail (*Lophortyx californica vallicola*), of which a careful ecological study was also made.

The significance of this piece of team research lies in the attempt to relate a wide field of observations, and the introduction of experimental enclosures for measuring the effects of rodent pressure on grassland, as well as in the improvement of census and marking methods for population research.

CHARLES ELTON

COUNTING SOIL ANIMALS

M. S. Gilyarov (1941). *Methods for taking censuses of the soil fauna.* Pochovedenie, No. 4: 48–76. (In Russian; summary in German. English translation available in the Bureau of Animal Population, Oxford University, Trans. 124.)

The author of this useful summary gives priority to Charles Darwin for doing quantitative work on soil animals. It therefore seems rather odd to say also that 'since the development of science and scientific methods is determined and stimulated primarily by practical demands, the working out of census methods for the soil

fauna has not unnaturally been initiated mainly by workers in applied zoology and entomology'. Darwin worked on earthworms because he was interested in finding out what earthworms do, how fast they turn the humus over, and whether they show intelligence in their behaviour. This is what he wrote on the last subject —a valuable proof of his general outlook on natural history and biology: 'As I was led to keep in my study during many months worms in pots filled with earth, I became interested in them, and wished to learn how far they acted consciously, and how much mental power they displayed.' No pressure here from the demands of the practical man or the officials of government. For no pressure of that kind is needed to produce classical work. On the contrary, the latter is itself a sort of time-bomb which some time later goes off in the minds of scientists and economic experts and leads to one of those sudden expansions of interest and activity which is so startling and seems in retrospect to have originated from one simple and luminous idea, an idea of the kind that will not come either by whistling for it or by merely laying out a huge research plan.

There is no outstanding book written yet about the soil fauna, but only a number of scattered papers and monographs, partly by general ecologists and partly by economic ecologists interested in agriculture and forestry. Gilyarov's summary is therefore welcome. He describes the methods suitable for each group, with simple line-drawings of the apparatus, and he even glances at soil rodents. The difficult question of how many samples to take is discussed, and some formulae given for finding out the answer. It seems to me that the real answer can only be determined after one has already attained some idea of the scale of populations present, and of their actual variability in density from one spot to another. This problem runs right through quantitative ecology, and experience teaches that no rule of thumb system will avoid pitfalls, but that one has to check the statistical value of the samples as the work goes along, and to be prepared to cut losses and repeat surveys where necessary. In U.S.S.R. a large number of wide surveys are evidently done, and for these some rules for collecting samples have to be devised. It would be interesting to know more about the scientific basis for these rules.

The bibliography seems to cover much of the non-Russian work, although the important monograph of Bornebusch on Danish forest soil animals is omitted; and it gives a useful opening onto Soviet literature on the subject.

CHARLES ELTON

THE STATE OF THE BRITISH FAUNA

F. Fraser Darling (1943). *Wild life of Britain.* 48 pp., 29 black and white pictures, 8 coloured plates. *Britain in Pictures* series, William Collins Sons and Co. Ltd., 48 Pall Mall, London, S.W. 1. Price 4*s.* 6*d.*

Careful selection was needed in order to write about the British fauna in forty-eight pages, especially with the pages so full of illustrations. The latter are intended to be the main attraction of the book, and the majority will certainly give pleasure to ecologists as well as to the general reader, as they form a selection from past books that are not readily consulted, and in most instances convey a clear impression of the environment of the animals, as with the excellent stag-beetle by Daniell (1809) which stands on a log overlooking a wooded gorge, or (1895) Smit's harvest-mice clustering round their nest in a stand of oats. In a brave attempt to show that the fauna of Britain does contain, besides the vertebrates, over twenty thousand insects and other invertebrates, there are also pictures of the emperor moth and the cabbage white butterfly, and their stages of development.

The text reviews the varied mosaic of British habitats, an extraordinary variety of conditions brought about by the highly condensed zones of geological formation that sweep over England in a south-west to north-east direction, the criss-cross relationship of rainfall and temperature zones, and the sharp gradients from coastal formations up to mountains, and besides these hundreds of islands mainly scattered along the west and north. The author rightly pleads for the maintenance and preservation of this variety of habitats and the animals that live in them, but has a reasonable discussion of the different motives that are likely to control our final policies on the matter. There is a brief summary of some historical changes, of the attempts to control wild life by passive edicts and by enclosure of remnant populations. Following this we have a rather rambling description of some British naturalists; but one has yet to detect in their magnificent contributions to ecology any very systematic trend. Rather one feels that each was a separate phenomenon not much influenced by the rest, and indeed sometimes hardly influenced by current thought. It is noticeable that, whereas the notes on past achievements mainly focus on individual men like White, Darwin, Harvie-Brown, Hudson and Eliot Howard, praise for modern work goes to little groups of workers, to organizations like the British Trust for Ornithology. This is a natural and inevitable trend, and does not at all imply that individuality is being submerged, only that the atmosphere of group research often supplies the specialized assistance that modern ecology depends upon.

On the subject of illustrations, the publishers have done us extremely well at the price, but one nevertheless gets the impression that nearly all natural history illustration except by photograph came to an end about 1900, except for some of Millais's and Thorburn's pictures, though these were the work of men already more than mature. Let us hope that colour photography does not blot out the wild-life artist's chances of coming back into practice, after the fashion of Tunnicliffe's excellent illustrations to other books by Fraser Darling. The most serious part of this book is the author's discussion of practical measures for wild-life preservation and management. He remarks ironically that 'probably no country has talked so much about wild-life protection, appointed committees to investigate the subject of national parks and so on, and done less.... We shall not get national parks without the expenditure of a goodly sum of hard cash and so far there is little evidence that the British Government has any intention of placing national parks among the earlier items of post-war reconstruction'—which is absolutely true. He makes an error in referring to a Committee of the House of Lords: this Committee on nature reserves only sat *in* the House of Lords (amidst extraordinary Old Testament murals which suggested no very dynamic thoughts of wild-life management), but had no administrative connection with it. This august legislative body has itself got no further in wild-life management than successfully promoting a county organization for slaying rabbits comparatively humanely, just before the present War.

Fraser Darling strongly points the need for ecological research as a basis for wild-life policy, and gives some notes upon the organizations at present capable of handling such research. We have a continuously rising curve of interest in natural history (the successful development of a very long national tradition), we still have the vegetation and animals, and we have the basis of an ecological science and the staffs for it. We now need a National Park and Nature Reserves policy in active being, and a national organized service to manage it.

CHARLES ELTON

A ZOOLOGY TEXT-BOOK

Tracy I. Storer (1943). *General zoology.* 798 pp., 551 text-figures and 5 coloured plates. McGraw-Hill Book Company Inc., New York and London. Price $3.75.

One of the features of this book that makes it feel fresher than most text-books of zoology is the number of original drawings that have been made specially for it; another is the obvious awareness of the ecological aspects of animal life that runs through the book. We have here, in fact, a work thoroughly suited to the mentality of a middle-twentieth century student, something that has emerged from the crushing atmosphere of the museum of comparative anatomy, and yet retains a sound respect for the importance of grammar (systematics) and historical background (evolution). There are 33 chapters, the first 11 of which deal with general subjects, including one on ecology. The rest divide the animal kingdom amongst them, in a systematic treatment illuminated by extremely intelligent comment and ingenious illustrations in the text. Taking some instances at random, we learn about the hosts of the Chinese liver fluke; there are pithy summaries of the hookworm and trichina situation; remarks on species introduced into the United States (such as snails, slugs, and earwigs); a note that *Enchytraeus albidus*—a small oligochaete worm—is grown in soil and used to feed aquarium fish and small laboratory animals; and another that the spring-tail *Achorutes nivicola* sometimes gets into the sap at sugar-maple camps; and similar comments that make the main framework of the description much more easy to comprehend, and sustain interest. A very useful feature is inclusion of the palaeontological range of different groups, which can usually only be dug out of geological books. On page 704 there is an interesting table of domesticated mammals, ranging from the white mouse and the mink to the yak and the fat-tailed sheep, with their countries of origin. To summarize: this text-book has retained a disciplined order, and an encyclopaedic content that appears on inspection to be generally reliable and accurate, without sacrificing interest.

The chapter on animal ecology mentions the chemical cycles in nature, the influence of physical factors on the range of tolerance and distribution of animals, the food cycle, cover, the inter-relations of animals competing for resources, populations, etc. The treatment here is inevitably very brief, and does little more than mention the existence of certain phenomena. But there are short lists of literature references at the end of this and other chapters, which provide further reading for the student. The author is to be congratulated on his successful attempt to integrate zoology for the student, and the publishers on charging such a low price.

CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the paper to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, B. M. Hobby, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Bassindale, R. (1943). 'Studies on the biology of the Bristol Channel. XI. The physical environment and intertidal fauna of the southern shores of the Bristol Channel and Severn Estuary.' J. Ecol. 31: 1–29.

Tide range and currents increase from Ilfracombe to Aust, the maximum range being nearly 50 ft. Turbidity is high, is maximum between Aust and Arlingham, and remains in the same zone at all seasons, moving up and down with the tides. It increases in winter, and with depth. Salinity is stable up to Aust in summer, but only to Weston in winter. The number of intertidal species of animals decreases fairly rapidly from Ilfracombe to Blue Anchor, whence it is nearly constant to Weston, above which it decreases very rapidly to below Gloucester.

Bassindale, R. (1943). 'A comparison of the varying salinity conditions of the Tees and Severn estuaries.' J. Anim. Ecol. 12: 1–10.

Detailed analysis of salinity conditions in relation to tides, seasons, and size and form of the estuaries show that the actual changes in the Severn are less than in the Tees, but the rates of change are greater. In the Tees the salinity is greater at the bottom than at the surface, while the Severn has no vertical salinity gradient. The most difficult conditions for animals and smallest numbers occur about half-way up the estuary in both rivers.

Brady, F. (1943). 'The distribution of the fauna of some intertidal sands and muds on the Northumberland coast.' J. Anim. Ecol. 12: 27–41.

The more abundant species usually have separate zones of maximum density due to period of exposure, degree of desiccation, percentage of silt, organic content, and competition for food. Variations of *p*H and salinity showed no correlation with distribution.

Stephenson, W. (1942). 'An ecological survey of a beach on the Island of Raasay.' Proc. Univ. Durham Phil. Soc. 10: 332–57.

The beach was surveyed for percentage of exposure between tides and certain critical levels were found at which algae, burrowing and surface living animals had upper or lower limits. The change in substratum and in slope of beach were found to explain some of these limits in burrowing animals, while others were apparently due to the ability of the different species to withstand different amounts of exposure. Two such groups are suggested: the 'sublittoral' species, best able to live where there was 5% or less exposure, and the 'inter-tidal' species living in exposures of 5–50%. The surface living animals had critical levels at 10, 25 and 60% exposure, the first of these coinciding with the lower limit of the boulder area.

Stuart, T. A. (1941). 'Chironomid larvae of the Millport shore pools.' Trans. Roy. Soc. Edinb. 60: 475–502.

Chains of pools from the sea to the land were progressively less saline and contained different dominant species of Chironomid larvae at densities up to 400 per sq. ft. It appeared, however, that salinity itself was not the limiting factor in the species composition of the pools. Besides other factors (such as predation) the oxygen available for respiration was important, and a relationship between the environment and the development of a closed tracheal system was established. Vertical zonation within a pool was also related to the respiratory mechanism: *Chironomus dorsalis* (well supplied with haemoglobin, but with a rudimentary tracheal system) in the oxygen-scarce mud; *Anatopynia varius* (with less haemoglobin and longer tracheal trunks) on the surface of the mud; *Cricotopus sylvestris* (no haemoglobin, but with large tracheal trunks) in the well-aerated surface water.

Sexton, E. W. (1942). 'The relation of *Gammarus zaddachi* Sexton to some other species of *Gammarus* occurring in fresh, estuarine and marine waters.' J. Mar. Biol. Ass. U.K. 25: 575–606.

G. zaddachi, an estuarine species, is a typical salinity indicator: the higher the salinity the fewer the hairs. Full description with 24 drawings: there has always been confusion with *G. locusta*.

Corbin, P. G. & Panikkar, N. K. (1942). 'The distribution of *Arachnactis albida* M. Sars in the Celtic Sea.' J. Mar. Biol. Ass. U.K. 25: 509–16.

The adult of this Cerianthid is unknown. Planktonic larvae were abundant in an area of high salinity about due south of south-west Ireland and due west of Land's End. They were absent from the low salinity area leading from St George's and Bristol Channels.

Cole, H. A. (1942). 'The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds.' J. Mar. Biol. Ass. U.K. 25: 477–508.

The American oyster pest has become established in four Essex rivers and on the Kentish flats off Whitstable. Tingles start feeding (preferably on oyster spat or barnacles) when the temperature rises above 11–12° C. and may destroy spat at the rate of 0·385 per tingle per day or 1*s*. 3*d*. per season. Also given: data on growth (tingles rarely exceed 4·3 cm. in shell height), sex ratios (more females are caught, especially during spawning) and control measures.

Lowndes, A. G. (1942). 'The displacement method of weighing living aquatic organisms.' J. Mar. Biol. Ass. U.K. 25: 555–74.

A specific gravity bottle is filled with sea water and its contents are poured into excess of silver nitrate, giving a precipitate of silver halide. If an organism had occupied part of the space in the bottle, the precipitate would have been less in proportion to the volume of the organism. From this difference, plus other, more simply obtained data, volumes of large and small aquatic organisms are obtained with an accuracy impossible by other means. The density of protoplasm in a sponge was calculated to be 1·0371 at 14·6° C.

(*b*) Fresh water

Browne, F. Balfour (1943). 'The distribution of *Agabus chalconatus* Panzer and var. *melanocornis* Zimm. (Col., Dytiscidae) in the British Isles.' Ent. Mon. Mag. 79: 124–5.

Gives a map showing the distribution of the water-beetle *Agabus chalconatus* and of its var. *melanocornis*. Appeals for further information.

Pearce, E. J. (1943). 'Water-beetles in old tree-stumps.' Ent. Mon. Mag. 79: 18.

Larvae, pupae and an adult of *Deronectes assimilis* taken in an old tree-stump fully two yards from the water's edge. Suggests that in wet seasons water-beetle larvae will travel a considerable distance to secure a suitable place for pupation.

Lloyd, Ll. (1943). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds. Part II.' Ann. Appl. Biol. 30: 47–60.

The specific fluctuations in the numbers of flies emerging from a bacteria bed are found to depend on weather influences reacting on *Metriocnemus longitarsus* and the worm *Lumbricillus lineatus*, two forms which dominate the upper region of the bed, the former being potentially predaceous. These deductions are based on nearly 8 years' observations.

Reynoldson, T. B. (1943). 'A comparative account of the life cycles of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henle in relation to temperature.' Ann. Appl. Biol. 30: 60–6.

The fecundity and reproductive rates over a temperature range of approximately 0–25° C. of these two cosmopolitan Enchytraeid worms are compared.

(c) Land

Medlicott, W. S. (1942). 'The natural history of Goathland Dale. II. The birds: an ecological study 1923–38.' 32 pp. Arbroath. Also (1940) Northw. Nat. 15: 28–40, 109–26.

List of 112 species arranged under main habitats of this upland district of Yorkshire.

Morley, A. (1943). 'Sexual behaviour in British birds from October to January.' Ibis, 85: 132–58.

A species list summarizing information available in this subject.

Donisthorpe, H. (1943). 'Coastal insects found inland.' Ent. Mon. Mag. 79: 125.

Records of the beetles *Broscus cephalotes, Harpalus serripes, H. picipennis, Crypticus quisquilius, Microzoum tibiale, Philopedon geminatus* and *Hypera fasciata*, which are usually and chiefly found on sandhills at the sea-coast, but also occur on the 'Breck' sands in Suffolk.

Dicker, G. H. L. (1943). 'Two species of coastal bugs (Hem., Lygaeidae) found inland.' Ent. Mon. Mag. 79: 118–19.

The suggestion that the bugs may be more closely related to a sandy habitat than actual coastal conditions is discussed.

Lewis, C. B. & Bletchly, J. D. (1943). 'The emergence rhythm of the dung-fly, *Scopeuma* (=*Scatophaga*) *stercoraria* (L.).' J. Anim. Ecol. 12: 11–18.

Laboratory experiments under normal daylight, constant light, and darkness, showed a diurnal rhythm of emergence reaching a peak between 09 and 14 hours, with practically none between 20 and 06 hours, and less pronounced peaks under constant light and dark. The sexes showed no difference in the hour of day, but the females seemed in general about a day in phase ahead of the males. Temperature appeared unimportant.

Staniland, L. N. (1943). 'A survey of potato aphides in the South-Western Agricultural Province.' Ann. Appl. Biol. 30: 33–42.

The distribution of the various species together with their fluctuations from year to year are discussed in relation to the proximity of winter hosts, altitude and meteorological conditions. Observations on their parasitism are also given.

Benson, R. B. (1943). 'More about the sawflies of Hertfordshire and Buckinghamshire and the list of British species (Hym., Symphyta).' Ent. Mon. Mag. 79: 7–12.

The number of British species is now assessed as 425, the total for Hertfordshire being 313 and for Buckinghamshire 230.

O'Mahony, E. (1943). 'Some Co. Kildare Coleoptera.' Ent. Mon. Mag. 79: 61.

Records the following beetles from a large example of the fungus *Polyporus squamosus* found growing on the trunk of a dead poplar: *Atheta nigricornis, A. pallidicornis, Autalia impressa, Leptusa haemorrhoidalis, Phloeonomus pusillus, Siagonium quadricorne, Abraeus globosus, Epuraea depressa, Lathridius nodifer, Ephistemus globulus, Cis boleti, C. bidentatus, Octotemnus glabriculus, Anthicus floralis, Bolitochara obliqua, Atomaria linearis, Cryptophagus dentatus, C. scanicus, Omalium rugulipenne.*

Donisthorpe, H. (1943). 'Some Middlesex Coleoptera.' Ent. Rec. 55: 18, 43–4, 61–2.

Localities with habitat notes.

Barton, L. F. (1943). 'Notes on *Crioceris lilii* Scop. (Col., Chrysomelidae).' Ent. Mon. Mag. 79: 19.

Life history of an exceedingly rare beetle which has suddenly occurred in numbers among cultivated lilies at Chobham.

See also **Donisthorpe, H.** (1943). Ent. Mon. Mag. 79: 120.

Day, F. H. (1943). 'Cumberland Odonata.' Ent. Mon. Mag. 79: 43–4.

Fourteen species of dragonflies occur in Cumberland. *Agrion splendens* has not previously been recorded in England farther north than Yorkshire.

Scott, H. (1943). 'Hibernation of *Chrysopa carnea* Stephens (Neur., Chrysopidae) in unusual numbers in a house.' Ent. Mon. Mag. 79: 63.

About three dozen specimens (including both sexes) of this green lacewing were found hibernating in November behind folding shutters in a country house in the Chilterns. A previous record of 126 specimens occurring together in a box camera is recalled.

Pickles, W. (1943). 'Further observations on the mound-building of ants.' Ent. Mon. Mag. 79: 53–5.

Lasius flavus and *L. niger* both build mounds of soil-particles, that of the former being a permanent one and that of the latter not so permanent, being used more as a nursery. The mounds of *L. flavus* are built of soil-particles solely and those of *L. niger* of soil-particles and other organic materials. *L. niger* also has a method of using grass-stems as scaffolding. The weight of soil used in building is given.

Harrison, J. W. Heslop (1943). '*Rhodites rosae* L. (Hym., Cynipidae) showing a preference for *Rosa rubrifolia* Vill. (Caninae, Subsect. Rubrifoliae) as a host-plant.' Ent. Mon. Mag. 79: 123.

Galls were restricted to members of the Caninae group of roses; ultimately the Cynipids deserted the usual Eucanine hosts and concentrated on *R. rubrifolia*, a highly specialized Canine form of Alpine origin. A plant closely resembling *R. rubrifolia* was synthesized by breeding from crosses between *R. Sherardi* (Caninae, Villosae) and *R. spinossima* (Spinosissimae). This may explain the evolution of *R. rubrifolia* and the behaviour of the Cynipids.

Niblett, M. (1943). 'The species of *Rhodites* causing pea-galls on *Rosa*.' Entomologist, 76: 11–15, 34–9.

Account of host plants, location of gall, etc. with some breeding and distributional records.

Perkins, R. C. L. (1943). 'Early spring Hymenoptera and other insects on Dartmoor in 1943.' Ent. Mon. Mag. 79: 130–2.

Records from the moorland at elevations of 900 to over 1000 ft. above sea-level.

Melrose, M. M. (1943). 'Larvae of *Pieris brassicae* in January.' Entomologist, 76: 82.

Records eight larvae of the large white butterfly in last instar in Hereford on 7 January 1943.

Thorpe, W. H. (1943). 'Larvae of *Pieris brassicae* L. (Lep., Pieridae) surviving the winter.' Ent. Mon. Mag. 79: 118.

Five larvae of the large white butterfly found feeding on 7 March 1943, after an exceptionally mild winter. All were parasitized by a Braconid of the genus *Apanteles*.

Milman, P. P. (1943). '*Pieris rapae* larvae in February.' Entomologist, 76: 122.

Two fully grown larvae of small white butterfly found on 6 February 1943, at Paignton. A male adult emerged from one of these on 5 March.

Johnson, C. G. (1942). 'Insect survival in relation to the rate of water loss.' Biol. Rev. 17: 151–77.

A critical review of the work of several authors. There is no simple relationship between survival or water loss and saturation deficiency, though drying power of the air is the most closely correlated of any measure of humidity.

(*d*) Small islands

Carpenter, G. D. Hale (1943). 'New records of insects and woodlice from Lundy Island.' Ent. Mon. Mag. 79: 121–3.

Extraordinary numbers of beetles, earwigs and woodlice were found under stones. The majority of beetles were Carabidae. There seemed no food available for so many carnivora and the suggestion is made that the beetles were sheltering under stones for the winter. Short lists are given of Coleoptera, Collembola, Orthoptera, Dermaptera, Hemiptera, Trichoptera, Lepidoptera, Hymenoptera, Diptera and Oniscoidea.

Harrison, J. W. Heslop (1943). 'The range of the greasy fritillary (*Euphydryas aurinia*) in the Hebrides and some possible deductions therefrom.' Ent. Rec. 55: 27.

Concludes that the Tiree-Coll group of islands was severed from Scotland prior to parting company with Ireland and received some of its fauna and flora from the latter county.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Corbet, A. S. & Tams, W. H. T. (1943). 'Observations on species of Lepidoptera infesting stored products.' Entomologist, 76: 26–30.

The first of a series of useful systematic papers. It is illustrated with a plate figuring species of *Aglossa* and *Achroia*.

Hinton, H. E. (1943). 'Observations on species of Lepidoptera infesting stored products. III. Characters distinguishing the larvae of the house moths, *Hofmannophila pseudospretella* (Staint.) and *Endrosis sarcitrella* (L.).' Entomologist, 76: 65–7.

Gives key and illustrations.

Collin, J. E. (1943). 'The British species of *Prosalpia* Pok. (Dipt., Anthomyidae).' Ent. Mon. Mag. 79: 83–6.

Includes key and notes on the taxonomy, distribution and habitat of the seven British species.

Collin, J. E. (1943). 'A revised table of the British species of *Argyra* Mcq. (Dipt., Dolichopodidae).' Ent. Mon. Mag. 79: 114–17.

These flies occur on damp bare ground such as on paths in woods and at the margins of streams and ponds. Separate keys to males and females are given with some distributional records.

Coe, R. L. (1943). '*Chamaemyia juncorum* Fall. and *C. herbarum* R.-D. (Dipt., Chamaemyiidae): a correction to my recent paper on the British species of the genus.' Ent. Mon. Mag. 79: 128–9.

Description and amended key for the determination of these flies.

Andrews, H. W. (1943). 'British Dipterological literature (III).' Ent. Rec. 55 (Suppl.): 1–5.

A bibliography of recent references to British flies arranged according to families.

Walton, G. A. (1943). 'The natural classification of the British Corixidae (Hemipt.).' Trans. Soc. Brit. Ent. 8: 155–68.

Establishes a new tribe, the Cymatiini, one new subgenus *Halicorixa*, and sinks *Sigara* as a subgenus of *Corixa*. Gives a list of the 35 British species. The paper is criticized by **China, W. E.** (1943), Ent. Mon. Mag. 79: 109–11.

China, W. E. (1943). 'New and little-known species of British Typhlocybidae (Homoptera) with keys to the genera *Typhlocyba*, *Erythroneura*, *Dikraneura*, *Notus*, *Empoasca* and *Alebra*.' Trans. Soc. Brit. Ent. 8: 111–53.

Includes keys, figures of genitalia, references and some ecological data.

Clark, E. J. (1943). 'Colour variation in British Acrididae (Orthopt.).' Ent. Mon. Mag. 79: 91–104.

Develops a method for the description of the colour forms of grasshoppers. Symbols are used to describe: (*a*) the colour, (*b*) the region, and (*c*) details of pattern.

Blair, K. G. (1943). 'Notes on some British species of *Strophosomus* (Col., Curculionidae).' Ent. Mon. Mag. 79: 133–7.

Key for the determination of these weevils.

Kimmins, D. E. (1942). 'Keys to the British species of Ephemeroptera with keys to the genera of the nymphs.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 7: 1–64.

There are 47 British species of this order which is of such interest to fishermen. Common names are given, also notes on the habitat and seasons of occurrence.

Grensted, L. W. (1943). 'The occurrence of *Hydropsyche saxonica* McLach. in Britain. With a new key to the British species of the genus *Hydropsyche* Pict. (Trich., Hydropsychidae).' Ent. Mon. Mag. 79: 35–8.

The known British material of *H. saxonica* is all from one locality, a rather fast-flowing narrow stream at Headington, Oxford.

Benson, R. B. (1943). 'British *Sciapteryx costalis* F. belong to the Atlantic sub-species *soror* Konow (Hym., Symphyta).' Ent. Mon. Mag. 79: 138.

This sawfly belongs to the Atlantic element in the British fauna, as does *Pristiphora denudata*. The Central European subspecies has a black instead of red subcosta to the fore-wing although the genitalia are apparently identical.

Nixon, G. E. J. (1943). 'A revision of the European Dacnusini (Hym., Braconidae, Dacnusinae).' Ent. Mon. Mag. 79: 20–34.

Includes keys and figures for the identification of these parasites.

3. PARASITES

Barnes, H. F. (1943). 'A further note on the unusual abundance of *Orgyia antiqua* L. (Lep., Lymantriidae).' Ent. Mon. Mag. 79: 47.

Vast numbers of vapourer caterpillars were feeding on bilberry on the mountains behind Penmaenmawr. Some 2500 caterpillars were kept: of these 1205 emerged (1137 females, 68 males); there also emerged 52 Tachinid parasites (*Carcelia gnava* and *Neopales pavida*) and 15 Braconids (*Rhogas geniculator*). The poor emergence figures are explained by the large numbers of caterpillars which dried up before spinning or after spinning and before pupation; the odd sex ratio suggests that the majority of the male caterpillars had already spun when the collection was made.

Blair, K. G. (1943). 'The host of *Chalarus spurius* Fall. (Dipt., Pipunculidae).' Ent. Mon. Mag. 79: 129.

This fly was bred from a paralysed Typhlocybid bug stored in a burrow in an old beech tree by the Crabronid wasp *Coelocrabro ambiguus*.

Whitehead, T. (1943). 'Some factors influencing the health of seed potato stocks in North Wales.' Ann. Appl. Biol. 30: 85–96.

Thomas, I. (1943). 'Ecology of potato aphides in North Wales.' Ann. Appl. Biol. 30: 97–101.

Doncaster, J. P. (1943). 'The life history of *Aphis* (*Doralis*) *rhamni* B.d.F. in eastern England.' Ann. Appl. Biol. 30: 101–4.

Gregory, P. H. (1943). 'The spread of potato virus diseases in the field.' Ann. Appl. Biol. 30: 104–5.

These four papers dealing with potato aphides form part of a symposium on potato virus diseases.

MacLeod, J. & Benson, H. J. Craufurd- (1941). 'Observations on natural populations of the body louse, *Pediculus humanus corporis* de G.' Parasitology, 33: 278–99.

Over 200 sets of undergarments were examined from men living in cheap hostels. The louse population on any individual tended to remain about the same. The chief factor influencing the counts was the frequency of change of underwear, i.e. the length of time given for lice to migrate from the outer garments. Shortly after a change of underwear the distribution of the louse population is abnormal, and there is a high proportion of adults to larvae. Lice hatched on the individual appear on the ninth day.

MacLeod, J. (1939). 'The ticks of domestic animals in Britain.' Emp. J. Exp. Agric. 7: 97–110.

Ixodes ricinus attaches itself to three different individuals in the course of its 1½ to 4½ years' life cycle. Typical densities are 15–100 females per sheep. The tick is most liable to mortality in its free-living stages and cannot survive where the microclimate does not provide sufficient moisture in summer. The thick mat of vegetation on rough grazings is thus an important factor in maintaining density. Besides tick-borne diseases sheep suffer other effects such as loss of blood. Control measures are discussed.

Gemmell, A. R. (1943). 'The resistance of potato varieties to *Heterodera schachtii* Schmidt, the potato-root eelworm.' Ann. Appl. Biol. 30: 67–70.

The numbers and size of cysts produced on the roots of different potato varieties and the number of larvae which emerged from the cysts were found to differ on the several varieties tested. It is concluded that the degree of resistance is specific to each variety and is physiological not anatomical.

4. FOOD AND FOOD HABITS

Collinge, W. E. (1943). 'Wild birds and home-grown food in Britain.' Nature, Lond. 151: 128–9.

Rooks feed largely on injurious insects; also the black-headed gull, whose greatest content of fish in the stomach was 12·85%. Recently the blackbird has been eating more insects and less fruit. Song- and missel-thrush take about twice the amount of injurious insects that they do fruit, and tits are negligible fruit eaters. Starling, house sparrow and pigeon need checking.

Gligg, W. E. (1943). 'The food of the wigeon, *Mareca penelope* Linn.' Ibis, 85: 82–7.

An examination of the literature shows that this species feeds to a hitherto unrecognized extent upon grass, browsing it like geese.

Hosking, E. J. (1943). 'Some observations on the marsh-harrier.' Brit. Birds, 37: 2–9.

General observations in breeding biology including an interesting account of the food brought to a single chick in the nest for 4 weeks. The most important items were 24 young pheasants, 21 young partridges and 15 rabbits.

Popham, E. J. (1943). 'Further experimental studies in the selective action of predators.' Proc. Zool. Soc. Lond. 112A: 105–17.

A continuation of previous investigation into its protective value of colour varieties in the Corixid *Sigara* (*Arctocorisa*). Using *Scardinius* (*Leuciscus*) as predator, it is shown that protection is most effective in a medium sized population, and declines when it is either too small or too large. Similarly when colour varieties of prey are mixed in different populations the most abundant are taken relatively more frequently. Selection of prey for size was also demonstrated by using different species of prey.

The author suggests that in the face of this demonstrable predator selection, polymorphism may be maintained by selective mating, which is confirmed by observation.

Smith, P. Siviter (1943). 'Damage by the earwig.' Entomologist, 76: 110.

Feeding on buds of *Clematis*.

Smith, W. Hawker- (1943). 'The food of the earwig.' Entomologist, 76: 63–4.

Records, among other observations, an earwig following a moth engaged in laying its eggs and eating the eggs as they were laid.

Tulloch, B. (1943). 'Habits of *Vanessa atalanta* and *Polygonia c-album*.' Entomologist, 76: 17.

The red admiral and comma butterflies belong to different genera yet have similar habits. Both remain on the wing in autumn longer than other butterflies. Both are greedy for sugar which the small tortoise shell never touches and the peacock rarely. Both visit ivy blossom and Buddleia flowers, but not lavender. Both seem to be attached to certain areas in the garden where they appear day after day.

Hinton, H. E. (1943). 'House moths feeding on dead insects in or near spider webs.' Entomologist, 76: 4–5.

The insect rejecta of spiders constitute numerous small and widely distributed food reservoirs which can be utilized by insects able to maintain themselves on dry animal matter.

Smart, J. (1943). '*Simulium* feeding on ivy flowers.' Entomologist, 76: 20–1.

On four consecutive days in September very large numbers of *Simulium salopiense* were observed feeding on the flowers of ivy. Males outnumbered females by about 6 to 1. The breeding place, the River Wye, is about half to one mile away from the point where the flies were seen. There were plenty of cattle in the neighbourhood which were not being exceptionally pestered by the flies at the time.

5. POPULATION STUDIES

Fisher, R. A., Corbet, A. S. & Williams, C. B. (1943). 'The relation between the number of species and the number of individuals in a random sample of an animal population.' J. Anim. Biol. 12: 42–58.

In this series of three mathematical papers, the first, by Corbet, shows that in a large collection of Malayan butterflies the rarer species fitted closely a logarithmic type of frequency distribution described by Fisher in

Part 3. In Part 2, Williams analyses the four-year collection of nocturnal Lepidoptera from the light-trap at Rothamsted, containing 15,609 individuals and 240 species, in relation to Fisher's mathematical theory, and shows that the calculated values are very close to those observed. The number of species shows a regular relation to the number of individuals for any given value of the parameter 'α', which it is suggested be called the 'index of diversity'. The value of 'α' has a regular seasonal change and is nearly the same in each year regardless of large differences in numbers caught. Two traps in different environments yielded samples with significantly different 'α' values.

A diagram (Fig. 8) is given from which any one of the three values, total number of individuals (N), total number of species (S), and index of diversity (α) can be found if the other two are known, as well as the standard error of α.

In Part 3, Fisher develops formulae on a theoretical distribution for the apparent abundance of different species, and presents special tables for facilitating the calculations.

Venables, L. S. V. (1943). 'Observations at a pipistrelle bat roost.' J. Anim. Ecol. 12: 19–26.

Counts about once a week at a country church near Oxford, the highest being 346, showed that the threshold temperature for emergence is usually above 40° F., the light on 64% of the observations was a Weston reading of 1·0 or under, and gusty winds seem to discourage emergence. Time of first emergence is around sunset in August, becoming later towards either end of the season.

Perry, J. S. (1943). 'Reproduction in the water-vole, *Arvicola amphibius* Linn.' Proc. Zool. Soc. Lond. 112A: 118–30.

An examination of 223 specimens showed a well-marked breeding season lasting from March to September. Young born early in the season will breed in the same year. Ovulation and embryo rates decrease during the year.

Ryves, B. H. (1943). 'An investigation into the roles of males in relation to incubation.' Brit. Birds, 37: 10–16.

Records of occasional brooding by males in species where the female mostly incubates.

Lack, D. (1942–3). 'The breeding birds of Orkney.' Ibis, 84: 461–84; 85: 1–27.

A detailed account of the present status of the Orkney bird fauna. An early section has an interesting account of the way southern species decline through England, Scotland, Orkney, Shetland, Faeroe and Finland and northern species in the reverse direction.

Alexander, W. B. (1943). 'The index of heron population 1942.' Brit. Birds, 36: 206–8.

The index shows a decline of about 5% in the figure for 1941. This was confirmed mostly in the south-west, north-west and eastern counties of England.

Bullough, W. S. (1942). 'Observations on the colonies of the arctic tern (*Sterna macrura* Naumann) on the Farne Islands.' Proc. Zool. Soc. Lond. 112A: 1–12.

Colonies of different sizes were investigated. In the larger ones the breeding cycle was more advanced than in the smaller ones. Nesting habitats varied considerably. Chicks learn their territory by experience and observe its boundaries until they are fledged.

Lack, D. (1943). 'The age of the blackbird.' Brit. Birds, 36: 166–75.

Ringing returns gave data on expectation of life and average length of life, which may be applicable to wild populations as a whole. The sample here examined showed a mortality of 30–50% of young before 1 August; 54% die before the next August and 40% in each following year. The expectation of life of an adult blackbird at all ages is about 1·9 years. The average length is about 1·6 years.

Lack, D. (1943). 'The age of some more British birds.' Brit. Birds, 36: 193–7, 214–21.

Data similar to those in the last Notice are given for starling, song-thrush, lapwing, woodcock, black-headed gull, lesser black-backed gull and cormorant.

Went, A. E. J. (1943). 'Salmon of the river Corrib, together with notes on the growth of brown trout in the Corrib system.' Proc. R. Irish Acad. B, 48: 269–98.

The two types of growth were again found in salmon: Type A, little or no growth in the spring before migration; Type B, a large amount. A minimum length of 5·2–5·5 in. was reached before migration.

Went, A. E. J. & Barker, T. S. (1943). 'Salmon and sea trout of the Waterville (Currane) River.' Sci. Proc. R. Dublin Soc. 23: 83–102.

Rate of growth of the smolts of sea trout in the sea is 3·2 in. per annum before spawning; half this rate afterwards. In the sea salmon rapidly overtake sea trout in length though while in fresh water the latter have the faster growth rate. Types A and B salmon smolts were again found.

Crombie, A. C. (1943). 'The effect of crowding upon the oviposition of grain-infesting insects.' J. Exp. Biol. 19: 311–40.

Experiments were carried out at constant temperature and humidity on highly inbred stock. In *Rhizopertha* the number of eggs laid per female per day (fecundity) falls off at densities above four wheat grains per beetle until the density reaches eight beetles per grain, after which the grains are no longer used as oviposition sites. The rate of feeding was reduced at densities of eight or more beetles per grain and may affect the fecundity in these cases. The depressing effect of overcrowding was shown to depend on the number of insects per grain and not on area or volume. Males contribute to the effect of density because they compete, for feeding purposes, for the grains in which the females oviposit. Fecundity returns to normal immediately upon return to a low density so the effect of crowding seems only temporary and behaviouristic. Egg fertility is not affected by density.

Populations of species which oviposit on different grains were combined (e.g. *Rhizopertha* on wheat and *Acanthoscleides* on beans). Except at very high density the effect of crowding on the fecundity of each species is the same as if it were present alone. There is no interference between them.

Populations of *Rhizopertha* and *Oryzaephilus* were combined, both of which oviposit on wheat grains. Fecundity falls with increasing density and the effect upon each species of the competition of members of the other species appears to be quantitatively identical with the competition of the same number of its own type.

The conditioning of the medium by the accumulation of waste products was avoided in the above experiments and its effects tested in a separate series. It reduced fecundity in a degree at first proportional to the amount of conditioning.

Conditioning and competition for oviposition sites apparently affect *oviposition* while starvation has a more radical effect on *egg formation* from which the insects only slowly recover.

Beirne, B. P. (1943). 'The biology and natural control of the larch-shoot moth, *Argyresthia laevigatella* H.-S.' Econ. Proc. R. Dublin Soc. 3: 130–49.

The degree of infestation seems to depend mainly on the amount of shelter afforded to the adult and not on the health or situation of the tree. In Ireland the most important factor in the natural control is insectivorous birds which destroy an average of 67% of the larvae and pupae; a further 10% are destroyed by fungi, nematodes, Hymenopterous parasites or other factors. The only species of Hymenopterous parasite bred was *Ephialtes* (*Pimpla*) *elegans* Woldst.

Kettlewell, H. B. D. (1943). 'A survey of the insect *Panaxia* (*Callimorpha*) *dominula* L.' Proc. S. Lond. Ent. Nat. Hist. Soc. 1942–3 (1): 1–49.

Small colonies of the scarlet tiger moth exist close to others, but pairing between them need seldom if ever take place owing to the habits of the imagines and the date of emergence, which is very much affected by immediate environment. Mutations in this species tend, therefore, to be localized. This paper considers all available information concerning habitat, life history, parasites, fertility, genetics, related species and subspecies, variation and British and Continental distribution. Two of the five plates are in colour.

Dicker, G. H. L. (1943). 'A swarm of *Heterogaster urticae* L. (Hem., Lygaeidae).' Ent. Mon. Mag. 79: 90.

At least 500 bugs (third instar nymphs except for eight adults) massed on two nettle heads. The gregarious habit is unusual in the Lygaeidae except when hibernating.

Mare, M. F. (1942). 'A study of a marine benthic community with special reference to the micro-organisms.' J. Mar. Biol. Ass. U.K. 25: 517–54.

Cores of bottom muds 5–15 cm. long were examined quantitatively for micro-organisms including bacteria. The surface layer is much richer than the deeper muds in total volume of living matter: 0·35 cu. mm./g. dry mud compared with 0·013 cu. mm. at 2·5–3·0 cm. depth. The greatest volume is contributed by planktonic diatoms and algae which are distinguished from the true bottom flora and fauna as the *microbenthos*. The term *meiobenthos* is proposed for copepods, nematodes, Foraminifera, etc. and *macrobenthos* for the larger organisms. The complex interrelationships are fully discussed.

Cheng, C. (1942). 'On the fecundity of some Gammarids.' J. Mar. Biol. Ass. U.K. 25: 467–75.

Comparative fecundity of different sized species was not related to body weight. However, within two species, *Marinogammarus marinus* and *M. obtusatus*, there was an increase in fecundity with size; also in *Gammarus duebeni* up to 19 mm., length, above which there was a negative correlation.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Dannreuther, T. (1943). 'Migration records, 1942.' Entomologist, 76: 73–80.

Insect immigration in 1942 was upon a small scale, except for the red admiral in Cornwall and the white butterflies in summer. Comparison is made with the maximum ever recorded and with 1925, a minimum year.

Shepherd, J. (1943). '*Papilio machaon* in Kent: the resultant broods.' Entomologist, 76: 16–17.

Specimens of the swallow-tail butterfly bred in Kent produced adults which belong to the Continental race and have no connexion whatever with our indigenous fenland form. In all probability the majority, if not all, of the *machaon* reported from Kent were of Continental origin.

Stewart, A. M. (1943). '*Nymphalis io* in Scotland.' Entomologist, 76: 16.

The peacock butterfly is extending its northward trend and has increased in numbers in the western counties of Scotland. In 1942 it was seen in numbers in the larval stage in the Isle of Arran.

Williams, C. B. (1943). 'Notes on some monarch butterflies captured in Great Britain.' Entomologist, 76: 1–3.

Records omitted from the author's list published in 1942, Trans. R. Ent. Soc. Lond. 92: 175–80.

Woollatt, L. H. (1943). '*Limenitis camilla* L. (Lep., Nymphalidae) in Devonshire.' Ent. Mon. Mag. 79: 138.

The white admiral butterfly has now reached Devonshire.

Tozer, D. (1943). 'Notes on the occurrence of *Platyrrhinus resinosus* Scop. (Col., Anthribidae) in the midlands.' Ent. Mon. Mag. 79: 62–3.

This beetle was previously only known to occur very locally in a few south-western counties of England, but in 1937 was found to be widely distributed in parts of Northamptonshire. Later it was obtained in Rutland and in eastern Leicestershire. In 1942 it appeared in Huntingdonshire. It has been found only on rotting logs and trees supporting the fungus *Daldinia concentrica*. These are chiefly ash, only rarely beech.

Harrison, J. W. Heslop (1943). 'The status of *Bombus smithianus* White (Hym., Apidae) on the Isles of Raasay, South Rona, Scalpay and Longay.' Ent. Mon. Mag. 79: 62.

The author believes that in 1933 or 1934, a movement of the humble-bee *B. smithianus* from the Outer Isles took place which reached as its maximum limits the shores of Western Ross. In the area thus occupied it flourished for some time; then, for some reason, possibly wholly or in part due to hybridization with *B. muscorum*, it failed to maintain itself and died out.

Popham, E. J. (1943). 'Observations on the migration of Corixidae (Hemiptera Heteroptera).' Entomologist, 76: 117–22.

There is a greater similarity of colour between the Corixids and the background in permanent habitats than in temporary ones. While Corixids of all species and colours migrate into a pond, there is a high emigration rate among those insects not adapted to the habitat, so that as time passes there is an increased proportion of those Corixids harmonizing with the background. Species like *Sigara nigrolineata*, *S. sahlbergi* and *Corixa punctata* which migrate readily are found in most habitats.

Collinge, W. E. (1943). 'Exotic woodlice in the British Isles.' Nature, Lond. 151: 394.

Trichorina thermophila, a Central American species, has been found at York, Kew, Newcastle, Winlaton Mill, Glasgow and Belfast; always in greenhouses. Five other introduced species are listed.

7. REPORTS OF ORGANIZATIONS

Freshwater Biological Association of the British Empire. Eleventh Annual Report for the year ending 31st March, 1943. 37 pp. Price to non-members, 1*s*. 6*d*.

The report gives brief accounts of investigation on fisheries, invertebrate animals, algae and lake deposits in progress at the Wray Castle laboratory. Whilst the war has inevitably restricted the work to some extent, all the main studies have made progress and those on perch and on lake deposits are of outstanding importance.

Hutton, J. A. (1943). 'Wye Salmon, 1943: Report of the Wye Board of Conservators.' Salm. Trout Mag. Lond. No. 108: 138–52.

No collection of scales for the determination of the age composition of the Wye Salmon stock in 1942 could be made, but as in the previous year, the weight statistics have been used for this purpose. The total catch of 3102 fish weighing 47,537 lb. was the smallest since 1938, but this appears to be due to shortage of labour and to travel difficulties rather than to a decline in the run. The most abundant fish were those which had spent between two and three years in the sea and which weighed from 7 to 20 lb. each.

Yorkshire Fishery District. Seventy-Sixth Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire (1942) (by **R. W. Ward**). 28 pp.

The total catch of salmon and migratory trout in this Fishery District in 1942 was 1402 fish weighing 8475 lb. The catch was higher than that of 1941 but lower than the previous ten years. Owing to scarcity of labour, the intensity of fishing has varied and it is doubtful whether the figures indicate fluctuation in the population. The report also includes notes on trout and other freshwater fish, fish passes, the Keld Head hatchery and pollution.